

On some hydroids (Cnidaria, Hydrozoa) from the Okinawa Islands, Japan

Peter Schuchert

Muséum d'histoire naturelle, route de Malagnou 1, 1208 Geneva, Switzerland. E-mail: peter.schuchert@ville-ge.ch

Abstract: This paper gives a systematic account of 32 hydroid species identified in a small collection originating from the Okinawa Islands. While most species are well-known from Japanese waters, three new species and five new records for Japan were found. Some not well known species are redescribed. Taxonomically important features of nearly all species are depicted. The new species are: *Schizotricha longinema* new spec., *Cladocarpus unilateralis* new spec., and *Macrorhynchia crestata* new spec. *Zygophylax pacifica* Stechow, 1920 is recognised as a new synonym of *Zygophylax cyathifera* (Allman, 1888). New records for Japanese waters are: *Lytocarpia delicatula*, *Macrorhynchia fulva*, *Caminothujaria molukkana*, *Zygophylax rufa*, *Thyroscyphus fruticosus*. The presence of *Zygophylax cervicornis* and *Aglaophenia cupressina* in Japanese waters are confirmed by new, fertile material.

Keywords: Leptothecata - Anthoathecata - marine benthic hydroids - Okinawa Islands - Japan - new species.

INTRODUCTION

Japan with its long complex coastline of more than 6000 islands spread over more than 22 degrees of latitudes, ranging from tropical to cool temperate seas, offers a formidable basis for a rich and diverse fauna of marine hydroids.

The first descriptions of hydroids from Japan were most likely published by Allman (1876) who described several Campanulariidae, Bonneviellidae, and Sertulariidae species. Inaba (1890, 1892) then initiated hydroid research in Japan itself and numerous publications by several authors followed. Of particular importance are the studies of Stechow, Jäderholm, Yamada, and Hirohito. A summary of the history on Japanese hydroid research and the pertinent references are given in Hirohito (1988). Most of these studies focused on Honshu and its adjacent islands. The small Okinawa archipelago is the most southerly Japanese prefecture and it belongs to a transition zone to the tropical regions found in the more southerly Philippines (Warm Temperate Northwest Pacific, Spalding *et al.*, 2007). In this region, at least some tropical hydroid species can thus be expected to occur. However, there are only few reports on hydroids from the Okinawa Islands. Yamada & Kubota (1987) provided the only available inventory, while Kubota (1987) and Hirose & Hirose (2012) added further details.

The present report gives an account of 32 species identified in a small collection of hydroids from the Okinawa Islands, mostly from around the islands of Kume and Okinawa. The samples were collected and

kindly given to me by Dr F. Sinniger (Japan Agency for Marine-Earth Science Technology).

MATERIAL AND METHODS

The hydroids were either collected by scuba diving or by dredging using a triangular dredge or a beam trawl. After collection and sorting, they were fixed in absolute ethanol. All samples described here are now in the invertebrate collection of the MHNG.

The specimens were examined with a dissecting microscope or a compound microscope using temporary or permanent preparations on microscope slides (see e. g. Gibbons & Ryland, 1989). Drawings based on material examined for this study and were usually made with the help of a *camera lucida*. The figures given in this publication thus allow making direct measurements of linear dimensions. A few photographs were obtained by combining pictures taken at different focusing levels (focus stacking) using the freely available software PICOLAY created by H. Cypionka (www.picolay.de).

Technical terms are generally used as explained in Cornelius (1995a, b), Millard (1975), Schuchert (1996, 2012), or Bouillon *et al.* (2006). The latter publication should also be consulted for genus and family diagnoses which are not given here. If not indicated otherwise, the supraspecific classification follows Schuchert (2015). The synonymy given here is incomplete and includes only the consulted publications. Usually at least one reference is given which has a complete synonymy.

Where possible, parts of colonies were used to extract DNA and to generate 16S sequences using the same techniques as given in Schuchert (2014). The results will be presented in a forthcoming publication.

Abbreviations:

| | |
|------|--|
| E | East |
| MHNG | Muséum d'histoire naturelle, Geneva, Switzerland |
| N | North |
| NMW | Naturhistorisches Museum Wien, Austria |
| S | South |
| SE | south-east |
| SW | south-west |
| UUZM | Zoologische Institute, University of Uppsala, Sweden |
| W | West |
| ZSM | Zoologische Staatssammlung München, Germany |

TAXONOMY

Order Anthoathecata Cornelius, 1992

Family Pennariidae McCrady, 1859

Genus *Pennaria* Goldfuss, 1820

***Pennaria disticha* Goldfuss, 1820**

Pennaria disticha Goldfuss, 1820: 89. – Brinckmann-Voss, 1970: 40, text-figs 43, 45-50. – Gibbons & Ryland, 1989: 387, fig. 5. – Schuchert, 1996: 142, fig. 85a-c. – Schuchert, 2006: 364, fig. 15. – Galea, 2008: 13, fig. 3E. – Calder, 2010: 65, fig. 43. – Calder, 2013: 7, fig. 1A.

Halocordyle disticha. – Millard, 1975: 41, figs 16C-G. – Hirohito, 1977: 2, fig. 1, pls 1-3. – Calder, 1988: 57, figs 43-45, synonymy. – Oestman *et al.*, 1991: 607, figs 1-18. – Hirohito, 1988: 28, figs 9a-d, pl. 1 fig. 1C.

Material: MHNG-INVE-60994; Japan, Okinawa Island, Mizugama, 26.35897°N 127.73856°E, 6 m; 13.05.2008; several infertile plumes, up to 8 cm. – MHNG-INVE-91094; Japan, Okinawa Islands, Okinawa Island, Convention Center, 26.283°N 127.73°E, 8 m; 05.06.2008. – Sample without voucher specimen, material used for DNA extraction; Japan, Okinawa Islands, Okinawa Island, Kin, Red Beach, 26.4453°N 127.9124°E, 8 m; 17.06.2008.

Diagnosis: Hydroid colony pinnate, monosiphonic, hydrocaulus and hydrocladia with terminal hydranths (monopodial); hydranths on short pedicels on upper side of the hydrocladia. Hydranths pear-shaped; tentacles of two types: in distal half of hydranth more or less capitate tentacles in one oral whorl and more in indistinct whorls below, on lower part of hydranth one aboral whorl of semifiliform to slightly capitate aboral tentacles; gonophores developing above aboral tentacles, developing into medusoids which may be liberated or not.

Medusoids elongated; manubrium not extending beyond umbrella margin; gonads completely surrounding manubrium; four radial canals; four permanently rudimentary tentacles, usually reduced to mere bulbs, without ocelli.

Description: See Schuchert (2006).

Type locality: Gulf of Naples (see Calder, 2013).

Distribution: Circumglobal in tropical and warm temperate waters; 0-29 m (Calder, 2010).

Solanderia secunda (Inaba, 1892)

Fig. 1

Dendrocoryne secunda Inaba, 1892: 98, figs 111-113.

Solanderia rufescens Jäderholm, 1896: 5, pl. 1 figs 1-2.

Ceratella minima Hickson, 1903: 114, pl. 13.

Ceratella crosslandi Thornely, 1908: 85.

Solanderia secunda. – Hirohito, 1988: 49, fig. 15. – Bouillon *et al.*, 1992: 12 pls 5-6, 10-12. – Watson, 1999: 13, fig. 9A-F. – Schuchert, 2003: 149, fig. 8. – Kirkendale & Calder, 2003: 164.

Solanderia minima. – Vervoort, 1967: 25, fig. 2, pl. 3 figs 3-4. – Millard & Bouillon, 1973: 16, fig. 2A-B, plate 1. – Millard, 1975: 59, fig. 21C-E.

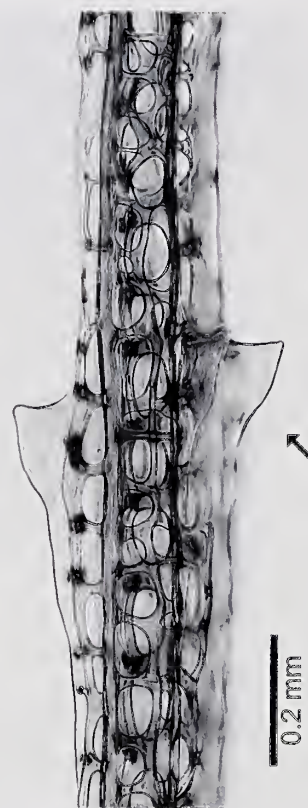


Fig. 1. *Solanderia secunda*, MHNG-INVE-91093, skeleton of terminal branch, soft tissues removed, arrow points at a pair of triangular hydrophores flanking originally a polyp (focus stacking image).

Material: MHNG-INVE-91093; Japan, Okinawa Island, Cape Hedo, 26.8719°N 128.2657°E, 18 m; 22.06.2008; one colony, 12 cm, elongate.

Diagnosis: Solanderiidae species with hydranth bases flanked by two parallel, broadly triangular periderm processes (hydrophores, Fig. 1).

Description: See Bouillon *et al.* (1992), Millard (1975, as *S. minima*), Watson (1999), or Schuchert (2003).

Type locality: Misaki, Japan (Inaba, 1892).

Distribution: Tropical and subtropical Pacific and Indian Ocean, reaching from Japan over Australia to South Africa and the Red Sea.

Family Balellidae Stechow, 1922

Remarks: Nutting (1906: 940) introduced the family name Tubidendriidae for his new genus and species *Balea mirabilis*. Because the genus *Balea* is preoccupied, Stechow (1919: 154) introduced the replacement name *Balella* Stechow, 1919. In order to have a correctly formed family name, Stechow later (1922: 142) also introduced the family replacement name Balellidae (see Calder, 2010).

Affinities and classification of Balellidae are difficult to resolve because the adult medusa of *B. mirabilis* remains unknown. Schuchert (2003), and Nutting (1906) earlier, suggested that affinities of the family were with Hydractiniidae. A preliminary comparison of the 16S sequence of *B. mirabilis* with hydrozoan sequences in the GenBank database (results not shown) clearly clustered it with various *Hydractinia* species. However, more sequences are needed to get a more reliable result (in prep.).

Genus *Balella* Stechow, 1919

Balella mirabilis (Nutting, 1906)

Fig. 2

Balea mirabilis Nutting, 1906: 940, pl. 2 fig. 3, pl. 7 figs 3-4. – Jäderholm, 1919: 4, pl. 1 figs 1-4.

Balella mirabilis. – Stechow, 1923b: 3. – Hirohito, 1988: 91, fig. 32a-c. – Schuchert, 2003: 140, fig. 2. – Calder, 2010: 29, fig. 17.

? *Balea irregularis* Fraser, 1938a: 13, pl. 1 fig. 5. – Calder *et al.*, 2003: 1204, synonym. – Calder *et al.*, 2009: 927, distinct species.

Material: MHNG-INVE-69638; Japan, Okinawa Islands, 26.32253°N 126.74598°E, 62-73 m; 14.11.2009; alcohol preserved 10 cm colony in two pieces, with gonozooids bearing advanced medusa buds; 16S sequence accession number LN810548.

Diagnosis: Hydroid colonies erect, branched, polysiphonic to the branch tips. All superficial tubes

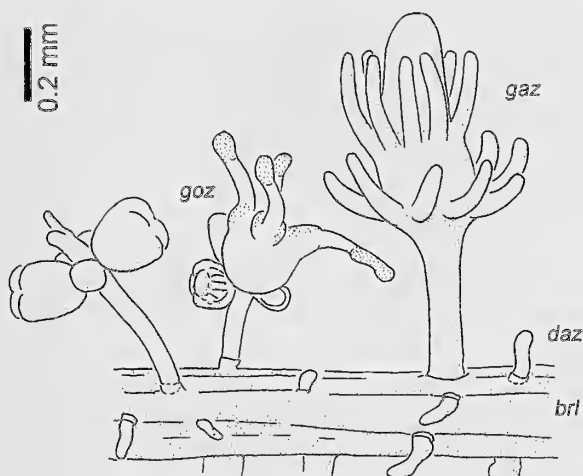


Fig. 2. *Balella mirabilis*, MHNG-INVE-69638, schematised part of branchlet (*brl*) bearing a gastrozoid (*gaz*), dactylozoids (*daz*), and two gonozooids (*goz*). The right gonozooid bears a medusa with its four tentacles everted.

can bear hydranths. Polyps polymorphic. Gastrozooids with club-shaped body and with two well separated whorls of tentacles. Gonozooids with either one tentacle or none, with one whorl of gonophores. Dactylozooids small, tentacle-like. Gonophores released as immature medusae. Young medusa with four filiform tentacles, manubrium simple. Adult medusa unknown.

Description: See Schuchert (2003).

Type locality: Hawaiian Archipelago, between Molokai and Maui, 232 m (Nutting, 1906).

Distribution: Hawaii (Nutting, 1906; Calder, 2010); Japan (Jäderholm, 1919; Hirohito, 1988), Indonesia (Schuchert, 2003); Galapagos Islands (Calder *et al.*, 2003). Depth range 49-538 m (Schuchert, 2003; Calder, 2010).

Remarks: This is a characteristic species and easy to recognise. It is widely distributed in the Pacific, but has not been reported frequently. The medusa buds in the present sample are developed to a point where they could be released (Fig. 2, *goz*). Many had their four tentacles already everted from the subumbrella. The nematocysts of the tentacles are concentrated at the ends, giving the tentacles a slightly capitate appearance. Nutting (1906) states that the branches of the colony are “partly covered with naked coenosarc, which occupies parallel open grooves on the surface.” In the present sample, hand-made cross-sections of branches showed no so naked coenosarc as e. g. in *Hydractinia* species. Perhaps Nutting mistook some adhering dactylozooids for external coenosarc.

The genus *Balella* currently comprises two species, *B. mirabilis* and *B. irregularis* Fraser, 1938. The status of the latter is not entirely clear, but Calder *et al.* (2009),

after re-examination of the type material of *B. irregularis*, recognise both species as valid. In *B. irregularis* from the Galapagos Islands, there are only four short tentacles in the proximal whorl. More samples are needed to confirm if this is a constant difference and not due to environmental influences.

Order Leptothecata Cornelius, 1992

Family Clathrozoidae Stechow, 1921

Remarks: When introducing the new genus *Clathroozoon*, Spencer (1891) also suggested placing it in a new family Hydrocerathinidae. This name is, however, incorrectly formed as it is not based on an existing genus name. Stechow (1921: 251) then introduced the family level names Clathrozoinae and Clathrozoidae. He also included the new genus *Clathrozoella* Stechow, 1921 in this family. The spelling Clathrozoidae used by Hirohito (1967: 1) must be considered a spelling error. Peña Cantero *et al.* (2003) then separated the genus *Clathrozoella* into a new family Clathrozoellidae Peña Cantero, Vervoort & Watson, 2003. This family belongs to the Order Anthoathecata, while *Clathroozoon* is clearly a Leptothecata.

Genus *Clathroozoon* Spencer, 1891

Clathroozoon wilsoni Spencer, 1891

Fig. 3A-H

Clathroozoon wilsoni Spencer, 1891: 123, pls 17-20. – Hirohito, 1967: 6, pls 1-7. – Hirohito, 1995: 8, fig. 1. – Watson, 2005: 503, fig. 38A.

Material: MHNG-INVE-69664; Japan, Okinawa Islands, SE of Kume Island, 26.2838°N 126.86587°E, 126-136 m; 12.11.2009; one fertile colony; 16S sequence accession number LN810549.

Diagnosis: Colony large, much branched, planar, resembling sea-fan. Skeleton a sponge-like periderm derived from coalesced stolon tubes, outside covered by membranous periderm. Hydrothecae arranged spirally on branchlets, almost completely sunken into skeleton of colony, sac-like, curved so that opening nearly parallel to surface, opening closed by conical operculum made of membranous, triangular flaps. Hydranths polymorphic, with gastrozooids, dactylozooids, and nematophores. Dactylozooids very long when extended, with a terminal whorl of capitate tentacles, retractable into hydrothecae identical to those of gastrozooids. Nematothecae tubular, short, arising from membranous cover of colony skeleton. Gonotheca sac-like, often in axils of bifurcating branches, covered by spongy perisarc. Gonophores are free medusoids, no manubrium, with velum, radial canals, eight short tentacles, gonads on radial canals (Hirohito, 1967).

Description: See Hirohito (1967, 1995).

Type locality: Port Phillip Bay, Victoria, Australia (Spencer, 1891).

Distribution: Japan (Hirohito, 1967, 1971, 1995; this study), Australia (Spencer, 1891; Watson, 2005).

Remarks: This is a rather unusual hydroid, its skeleton being very reminiscent of the Solanderiidae (comp. Fig. 1). However, the hydrothecae with an operculum (Fig. 3E) are evidence enough to identify them as Leptothecata. The hydrothecae are almost entirely sunken in a sponge-like lattice (Fig. 3A-E) which is derived from bundled, stolon-like coalesced tubes. Along the surface there are longitudinal ridges (Fig. 3A). Unlike in the Solanderiidae, the surface of the whole colony is covered by a thin, membranous periderm layer (Fig. 3D, F). This membrane is regularly perforated by chimney-like nematothecae (Fig. 3F).

Family Lafoeidae Hincks, 1868

Genus *Acryptolaria* Norman, 1875

Remarks: See Peña Cantero *et al.* (2007) for a recent revision and review of the genus. Descriptions of more species and a key to the species of the western Pacific are given in Peña Cantero & Vervoort (2010).

Acryptolaria pulchella (Allman, 1888)

Fig. 4A-B

Cryptolaria pulchella Allman, 1888: 40, pl. 19 figs 2 & 2a. – Clarke, 1894: 76. – Nutting, 1906: 947. – Stechow, 1913: 112.

Acryptolaria pulchella. – Peña Cantero *et al.*, 2007: 261, figs 13, 16E, 18E. – Peña Cantero & Vervort, 2010: 318, figs 26, 30, 32I.

Material: MHNG-INVE-69666; Japan, Okinawa Islands, SE of Kume Island, 26.3283°N 126.71595°E, 93-101 m; 19.11.2009; sterile colony.

Diagnosis: Similar to the well-known *A. conferta* (Allman, 1877), but terminal branches straight and not zig-zag, diameter of hydrotheca larger than 0.23 mm. For more criteria see key in Peña Cantero & Vervoort (2010).

Description: Colony fan-shaped, planar, 7 cm in height, stems and larger branches polysiphonic, monosiphonic branches slightly zig-zag. Hydrothecae alternate, in two opposite rows, in plane of colony. Hydrothecae tubular, about 1 mm long, about 2/3 of adcauline side adnate to branch (in monosiphonic part), evenly curved (ca. 70-80°), basal part somewhat narrowing, no diaphragm, opening circular, diameter 0.32-0.36 mm, renovations of margin frequent. Coenosarc with numerous large nematocysts (4-5)x(16-19)µm. Gonosome not observed.

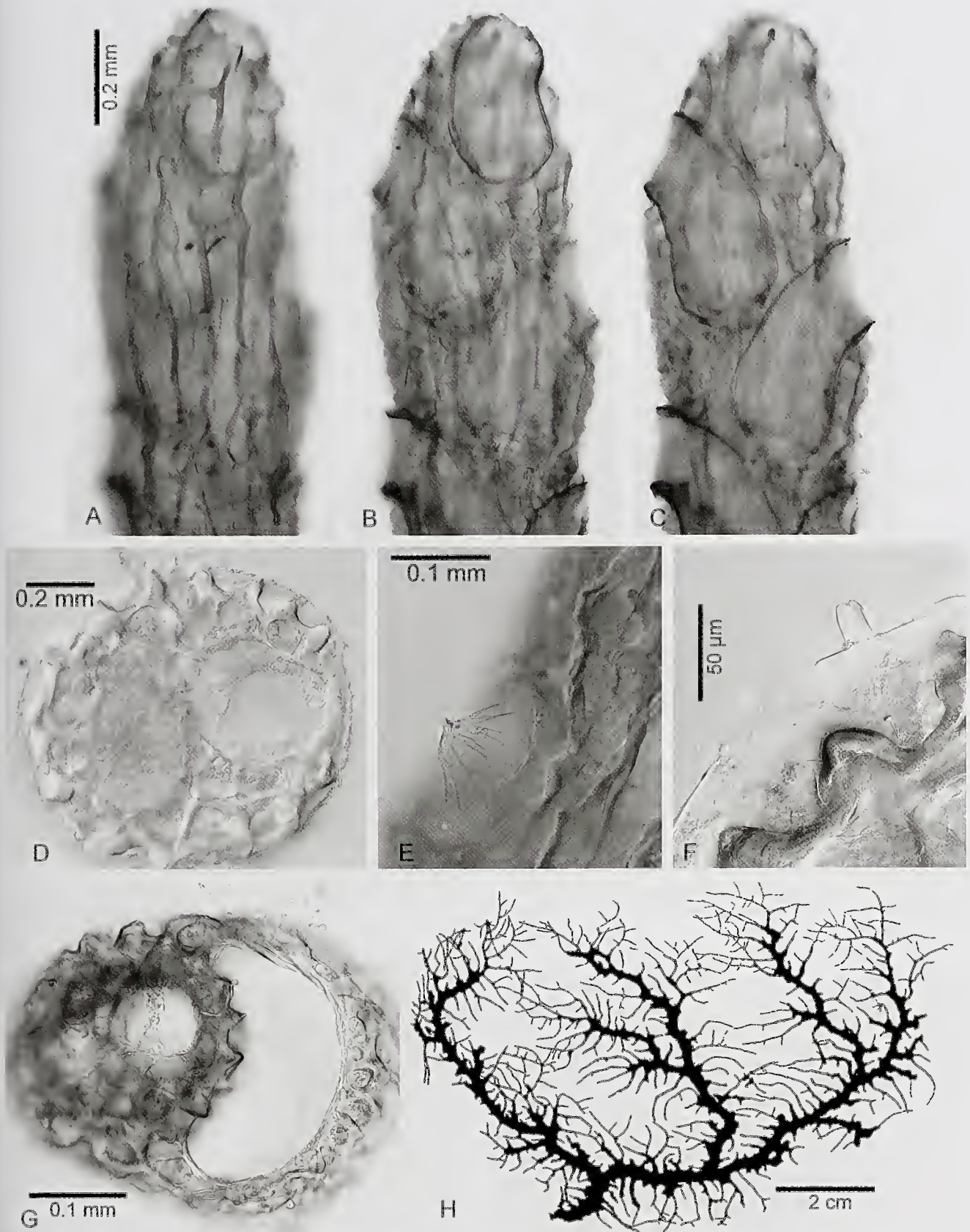


Fig. 3. *Clathrozoön wilsoni*, MHNG-INVE-69664. (A-C) Terminal region of a branch seen in three different focusing planes (surface, subsurface, middle of branch). Hydrothecae are visible in B and C. (D) Cross-section of branch, note membranous layer on surface. (E) Oblique view on branch showing a conical operculum. (F) Higher magnification of cross-section of branch. The outer membrane is somewhat detached and shows a short nematothecae without soft tissue. (G) Cross-section of branch with a gonothecae (at right, void). (H) Colony silhouette.

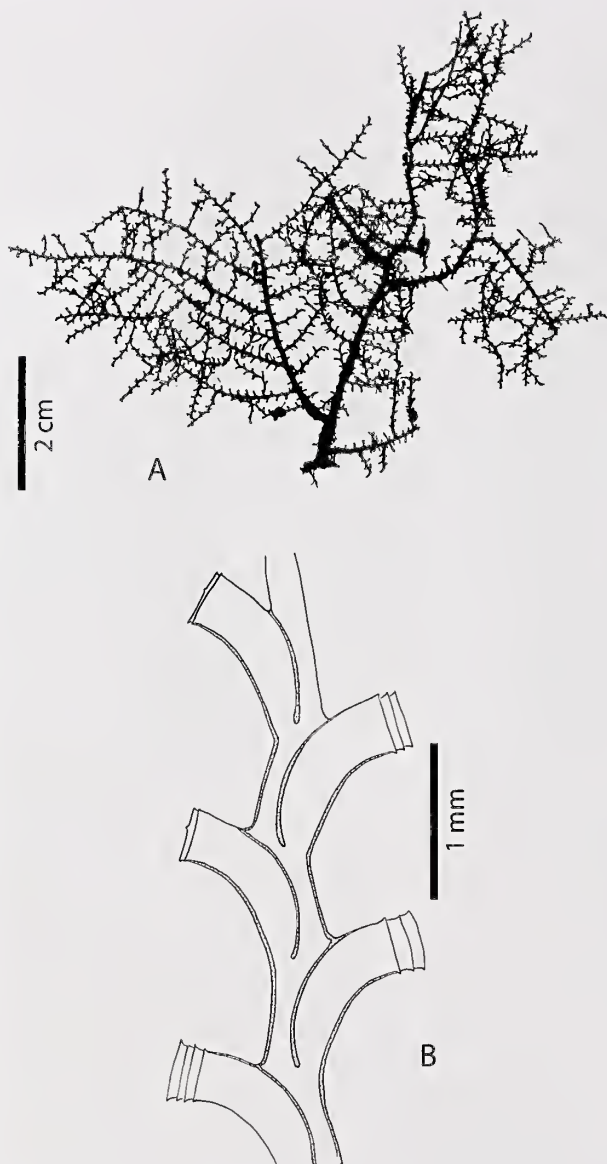


Fig. 4. *Acryptolaria pulchella* MHNG-INVE-69666. (A) Colony silhouette. (B) Monosiphonic part of distal branch.

Type locality: Honolulu, 36-72 m (Allman, 1888).

Distribution: Hawaii (Allman, 1888; Nutting, 1906); Pacific coast of Panama (Clarke, 1894); Sagami Bay, Japan (Stechow, 1913), Philippines (Peña Cantero & Vervort, 2010). Depth range 36-836 m.

Remarks: Peña Cantero & Vervort (2010) described and redescribed numerous *Acryptolaria* species from the western Pacific (New Caledonia to Philippines). The present material from Japan did not match precisely any of their descriptions, although *A. pulchella* comes close. The present colony differed from the type specimen and their Philippine material in having larger diameters of the hydrothecae (0.32-0.36 versus 0.23-0.28 mm) and smaller supplementary nematocysts (16-19 μ m versus 20-23 μ m). With our current knowledge it is impossible

to decide if these differences represent intraspecific or interspecific differences. I tend more towards the former and because the species has already been reported from Japan by Stechow (1913), the present material was thus identified hesitatingly as *Acryptolaria pulchella* (Allman, 1888).

Genus *Cryptolaria* Busk, 1857

Remarks: See Ralph (1958), Rees & Vervoort (1987), Hirohito (1995), or Vervoort & Watson (2003) for species and details.

Cryptolaria pectinata (Allman, 1888)

Fig. 5A-B

Perisiphonia pectinata Allman, 1888: 45, pl. 21 figs 2, 2a-b. – Pictet & Bedot, 1900: 18, pls 4-5. – Ritchie, 1911: 835, pl. 87 fig. 2.

Perisiphonia chazaliei Versluys, 1899: 32, figs 2-4.

Acryptolaria pectinata. – Stechow, 1925: 448, figs 20-21.

Eucryptolaria pinnata Fraser, 1938b: 140, pl. 20 fig. 9. – Rees & Vervoort, 1987: 50, synonym.

Cryptolaria pectinata. – Ralph, 1958: 320, figs 5g-j & 6g-j. – Millard, 1975: 174, fig. 58A-F. – Rees & Vervoort, 1987: 49. – Ramil & Vervoort, 1992a: 52, fig. 10d. – Hirohito, 1995: 109, fig. 30d-e, pl. 7 fig. A. – Vervoort & Watson, 2003: 54. – Calder, 2013: 20, fig. 5f, taxonomy.

Euperisiphonia rigida Fraser, 1940: 579, pl. 33 fig. 7. – Calder *et al.*, 2009: 979, synonym.

Material: MHNG-INVE-69654; Japan, Okinawa Islands, SE of Kume Island, 26.2776°N 126.89145°E, 151-160 m; 12.11.2009; one fragmented plume with coppinia.

Diagnosis: *Cryptolaria* species with stem heights reaching 12 cm, with two longitudinal rows of alternate hydrothecae, hydrothecae with distal 1/2 to 1/3 part curved at right angle and protruding out of polysiphonic branches (at least as much as the diameter of hydrotheca), hydrothecal rim often renovated. Nematothecae present on stem and hydrocladial tubes in variable numbers, tubular, with undulated walls.

Gonosome a coppinia, being an oval mass of gonothecae attached around stem or branches. Gonothecae close so that lateral walls adnate (Fig. 5C), elongated bottle-shaped, distally with a shoulder and narrowing into a neck, the latter may be or not drawn out into one or two opposite hood-like structure, opening by means of either a single or two opposed, laterally directed openings. Slender tubes (nematophorous ramuli, Fig. 5D) arise between the gonothecae and project beyond the general surface of the coppinia, the distal free end of these tubes are branched or not, with one or more nematothecae along the branch.

Description: See Ralph (1958) or Hirohito (1995) for illustrations and detailed descriptions. Diameters of

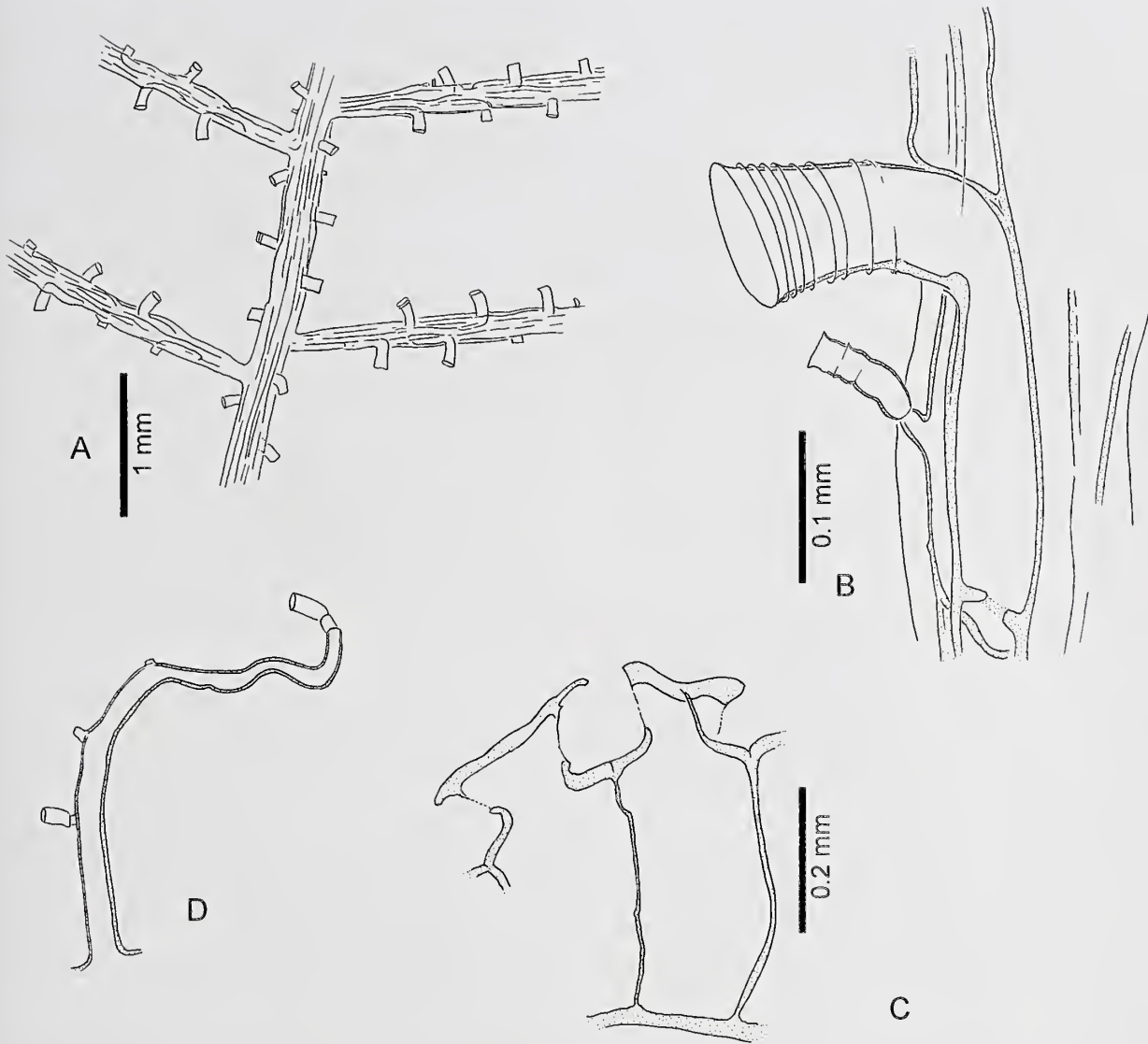


Fig. 5. *Cryptolaria pectinata*, MHNG-INVE-69627. (A) Part of stem and hydrocladia. (B) Hydrotheca and nematotheca. (C) Vertical section through coppinia showing one complete (right) and one incomplete gonotheca (left). (D) Protective ramule of coppinia, same scale as C.

hydrothecae in present material about 80 μm , spacing of hydrothecae in one row about 0.5 mm, gonothecae 0.45 mm high, with two pointed processes, the whole neck region resembling the form of an anvil (Fig. 5C).

Type locality: New Zealand, off East Cape, 37.5667°S 179.3667°E, depth 1278 m (Allman, 1888).

Distribution: The geographical distribution includes areas in the Atlantic-, Indian-, and Pacific Oceans in depths of 49–1280 m (Vervoort & Watson, 2003).

Remarks: The present material matched well the description given by Hirohito (1995), except that there were fewer nematothecae. Their number is variable (Vervoort & Watson, 2003) and of no systematic importance.

Ralph (1958) depicts gonothecae from the type specimen

which have their distal region drawn out into a hood-like structure with an opening at its base. Stechow (1925), having material from the north-eastern Atlantic, observed two types of gonothecae: either with one pointed process or with two. His conclusion that this reflects a sexual dimorphism, with the latter form being females, was refuted by Ralph (1958). The present material had processes with two points, the whole neck region resembling the form of an anvil, conforming to the observations of Millard (1975) and Hirohito (1995). Nematoporous ramules are also present in the material from Okinawa. Calder *et al.* (2009) found them lacking in the type material of *Euperisiphonia rigida* Fraser, 1940, which Calder *et al.* (2009) consider conspecific with *C. pectinata*.

Genus *Lafoea* Lamouroux, 1821

Lafoea dumosa (Fleming, 1820)

Fig. 6A-B

Sertularia dumosa Fleming, 1820: 84.

Lafoea dumosa. – Cornelius, 1975: 385, fig. 4, synonymy. – Cornelius, 1995a: 261, fig. 60. – Hirohito, 1995: 126, fig. 36a-c, pl. 8 fig. A. – Schuchert, 2001: 67, fig. 54A-D.

Material: MHNG-INVE-69627; Japan, Okinawa Islands, SE of Kume Island, 26.2451°N 126.85728°E, 179-192 m; 20.11.2009; sterile colony. – MHNG-INVE-69652; Japan, Okinawa Islands, SE of Kume Island, 26.2624°N 126.857°E, 150-168 m; 12.11.2009; sterile colony.

Diagnosis: *Lafoea* forming erect, polysiphonic colonies, hydrothecae 0.5-0.6 mm in height (valid for Japanese waters only).

Description: See Cornelius (1995a).

Type locality: Arboath, Angus, Scotland (Cornelius, 1975).

Distribution: Near-cosmopolitan, being widely distributed in Atlantic, Pacific, and Indian Oceans, penetrating both in Arctic and Antarctic regions (Vervoort & Watson, 2003).

Remarks: The two examined colonies had hydrothecae with a more or less distinct pedicel (Fig. 6A-B) and they also possessed large type (22 µm) of nematocysts. Schuchert (2001) found that the presence of a pedicel correlates with the large type of nematocysts (>21 µm), while colonies with sessile hydrothecae had usually

smaller nematocysts (< 16 µm). This is a strong indication that two separate species are involved. Preliminary molecular data (Moura *et al.*, 2011) confirmed this idea and more studies are clearly needed to disentangle the complex situation of the numerous nominal *Lafoea* species.

Genus *Zygophylax* Quelch, 1885

Remarks: Although most species of this genus have been redescribed or revised (e. g. Cornelius, 1975; Hirohito, 1995; Rees & Vervoort, 1987; Antsulevich, 1988; Gibbons & Ryland, 1989; Ramil & Vervoort, 1992a; Altuna Prados & Alvarez-Claudio, 1994; Vervoort & Watson, 2003; Schuchert, 2003; Calder *et al.*, 2009; Altuna, 2012), many species remain difficult to distinguish and a comprehensive, worldwide revision using morphological and molecular data is needed. Most species are only reliably identifiable when fertile, as the coppinia offer often the only distinctive characters.

Zygophylax cervicornis (Nutting, 1906)

Fig. 7A-H

Lictorella cervicornis Nutting, 1906: 946, pl. 4 fig. 1, pl. 10 figs 5-9.

Not *Lictorella cervicornis*. – Fraser, 1918: 134, pl. 2 fig. 3. – Fraser, 1937: 123, pl. 26 fig. 141. [= *Z. convallaria*]

Zygophylax cervicornis. – Jäderholm, 1919: 10. – Leloup, 1938: 10. – Rees & Vervoort, 1987: 69. – ? Vervoort & Watson, 2003: 72, fig. 10D-F.

Not *Zygophylax cervicornis*. – Hirohito, 1983: 28-29, fig. 9. [= *Z. convallaria*, see Hirohito, 1995]

Material: MHNG-INVE-69625; Japan, Okinawa Islands, S of Kume Island, 26.2454°N 126.8174°E, 141-165 m; 20.11.2009; fertile colony, likely female. – MHNG-INVE-69628; Japan, Okinawa Islands, S of Kume Island, 26.2451°N 126.8573°E, 179-192 m; 20.11.2009; sterile.

Diagnosis: *Zygophylax* forming much branched colonies reaching 10 cm in height, stem and hydrocladia bases polysiphonic, perisarc of stem and branches pale yellow.

Hydrotheca slender, deeply campanulate, about three times as long as wide, slightly curved, pedicel separated from apophysis by distinct node. Nematothecae variably present on apophyses of hydrothecae, short, barrel-shaped. Gonothecae in coppiniae, loosely aggregated and not in contact with each other, numerous protective branches which branch and coalesce profusely, thus forming a dense, three-dimensional lattice over the gonothecae. Gonothecae with irregular shape, approximately an inverted cone, 2-3 subterminal openings directed sideways, opening mostly not on tubular necks, sometimes on broad and short tubular extensions.

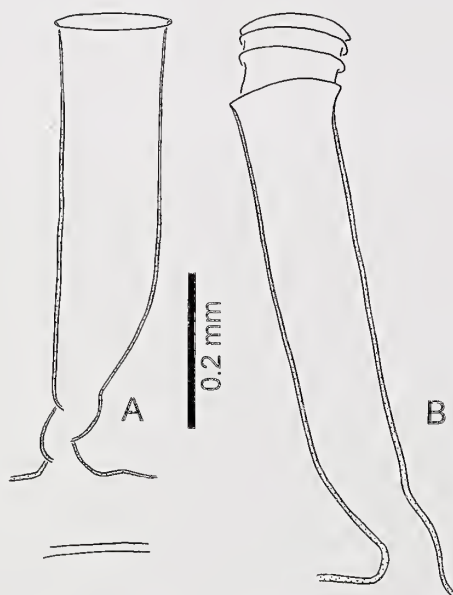


Fig. 6. *Lafoea dumosa*, hydrothecae. (A) MHNG-INVE-69652. (B) MHNG-INVE-69627.

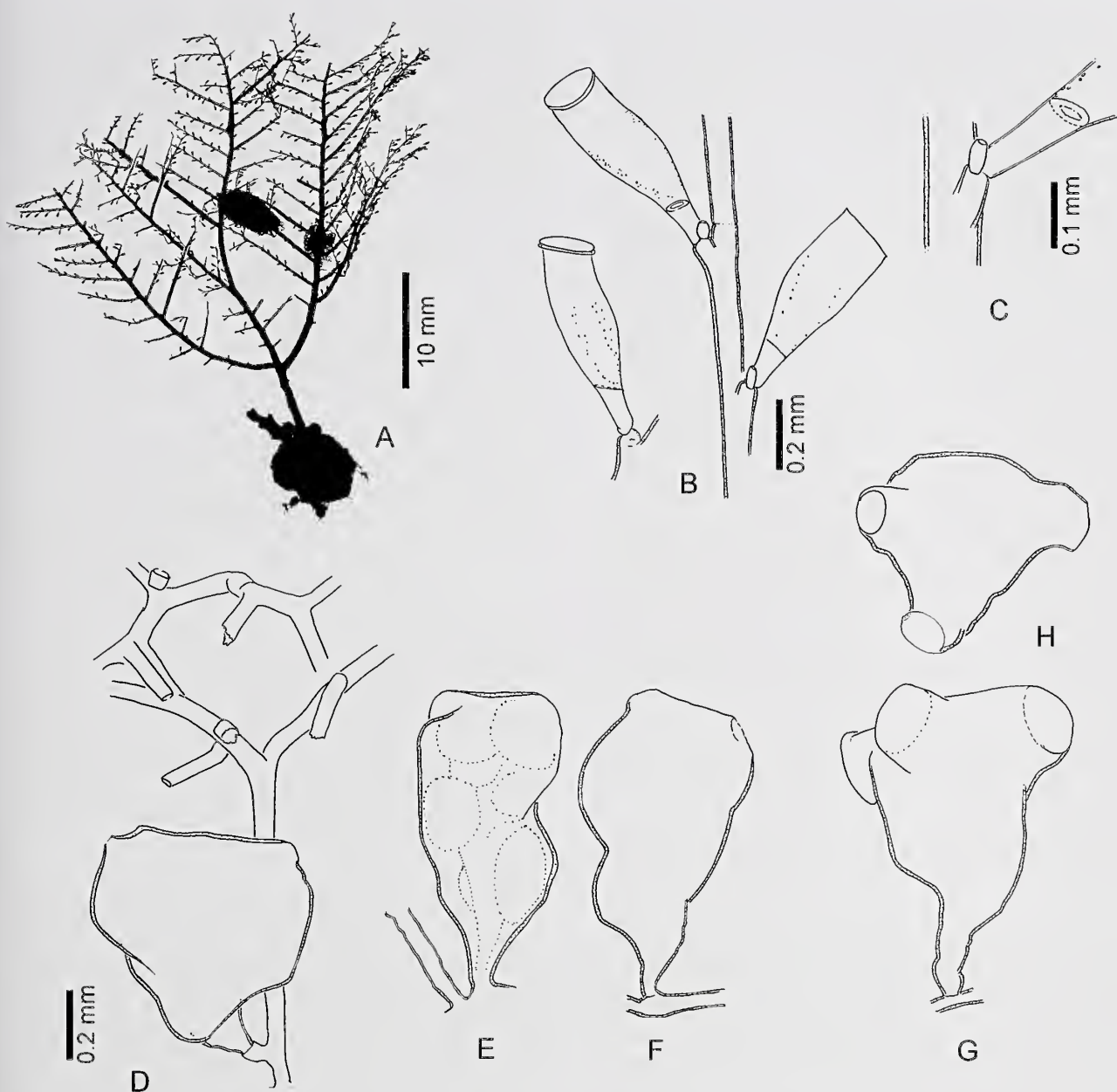


Fig. 7. *Zygophylax cervicornis*, MHNG-INVE-69625. (A) Colony silhouette. (B) Hydrothecae from the hydrocladia, note the two rows of perisarc dots. (C) Apophysis with nematotheca and pedicel of hydrotheca. (D) Gonotheca and some protective tubules. (E-F) Typical gonothecae in lateral view, in E the outline of the soft tissue is shown. (G) Gonotheca with openings on short, thick necks, lateral view. (H) Same gonotheca as in G in axial view from above.

Description (Okinawa material): Colonies erect, pinnate, up 9 cm (Fig. 7A); stems branching extensively in roughly one plane, thick, polysiphonic, bearing two rows of branches (hydrocladia). Perisarc of stem thick and firm, horny brown-yellow in colour.

Stem composed of an axial tube and several parallel accessory tubes, all without distinct nodes, apophyses of hydrothecae hidden by accessory tubes, stem hydrothecae often lost.

Hydrocladia subopposite, often not clearly distinguishable

from branched stem, polysiphonic except towards the ends. Hydrothecae of hydrocladia alternate, in two rows, not in the same plane as the branched stem but directed obliquely in relation to stem plane.

Basal part of hydrotheca separated from apophysis by distinct node (Fig. 7C). Hydrotheca deeply campanulate, rather elongate, about three times as long as wide, depth from diaphragm to rim 0.45-0.6 mm, gently curved, sometimes with S-like curvature (Fig. 7B) or straight, diaphragm with large, circular opening. Pedicel (basal

node to diaphragm) about 1/5 of total height. Perisarc of hydrotheca firm, gradually thinning out along hydrothecal wall. Hydrothecal aperture circular, slightly everted and often with 1-3 renovations. On inside of hydrotheca two irregular rows of dot-like perisarc thickenings (desmocytes) (Fig. 7B).

One nematotheca on most apophyses bearing the hydrothecae (Fig. 7C), often missing (lost?). Nematothecae small, lateral walls bulging and thus barrel-shaped, with circular opening, perisarc very thin. Gonothecae in coppiniae wrapping the stem (Fig. 7A), loosely aggregated and not in contact with each other, arising from thin tubules. Coppinia with numerous additional protective tubules which branch and coalesce profusely, thus forming a dense, three-dimensional lattice over the gonothecae, nematothecae not apparent. Gonothecae with irregular shape, approximating an inverted triangle (Fig. 7D-G), 2-3 openings subterminal and directed sideways, opening mostly not on tubular necks, sometimes on broad and short tubular extension (Fig. 7G-H). Female gonothecae with up to eight eggs or embryos.

In addition to the small (ca. 6 µm) tentacular nematocysts, there are a few large, oval nematocysts of 16-18 µm length.

Type locality: Between Islands of Molokai and Maui, Hawaii, 21.0444°N 156.739°W, 252-256 m (Nutting, 1906).

Distribution: Hawaii, Japan, New Zealand (Vervoort & Watson, 2003).

Remarks: *Zygophylax cervicornis* has been reported several times for Japan (Jäderholm, 1919; Leloup, 1938; Hirohito, 1983) and the Pacific coast of North America (Fraser, 1918, 1937). However, all these records were based on infertile material and hence these identifications must be considered doubtful. Hirohito (1983) mentions that he had seen fertile material from Sagami Bay, which, however, had gonothecae that differed from Nutting's (1906) *Z. cervicornis*. Later, Hirohito (1995) identified this material as *Z. convallaria* (Allman, 1877). Following Hirohito, Vervoort & Watson (2003) then referred all these former records to *Z. convallaria*. *Zygophylax cervicornis* and *Z. convallaria* are very similar and Vervoort (1972) synonymised the two names. Later, Rees & Vervoort (1987) kept them distinct again and also Hirohito (1995) regarded them as distinct. *Zygophylax cervicornis* has rather distinct gonothecae (Fig. 7D-F) lacking the relatively long horizontal necks of *Z. convallaria* (see Vervoort, 1972 and Hirohito, 1995 for a description of *Z. convallaria*). Only sometimes there are thick, short necks present as shown in Fig. 7G-H. Another difference is found in the protective tubules of the coppinia: they are sparse in *Z. convallaria* and very much developed in *Z. cervicornis*. The present material

agrees rather well with Nutting's (1906) description of both the trophosome and the gonosome.

The two rows of perisarc dots along the inside of the hydrotheca have not been reported by other observers and could be a unique feature. They are only visible in specimens which have been cleaned by digesting the soft tissues with a proteinase (as used for DNA extractions).

Zygophylax cyathifera (Allman, 1888)

Fig. 8A-B

Lictorella cyathifera Allman, 1888: 36, pl. 11 figs 3 & 3a. – Billard, 1910: 7, fig. 2.

Zygophylax cyathifera. – Rees & Vervoort, 1987: 62, figs 11 & 12a-c.

Zygophylax biarmata. – Stechow, 1913: 114, fig. 88. [not *Zygophylax biarmata* Billard, 1905]

Zygophylax pacifica Stechow, 1920: 19. **new synonym**

Zygophylax pacifica. – Stechow, 1923c: 141. – Leloup, 1938: 10. – Vervoort, 1941: 198. – Rees & Vervoort, 1987: 74. – Hirohito, 1983: 29, fig. 10. – Hirohito, 1995: 142, fig. 43e-f, pl. 9 fig. B.

Material: MHNG-INVE-69626; Japan, Okinawa Islands, S of Kume Island, 26.2451°N 126.85728°E, 179-192 m; 20.11.2009; fertile colony. – MHNG-INVE-69648; Japan, Okinawa Islands, S of Kume Island, 26.2624°N 126.857°E, 150-168 m; 12.11.2009; fertile colony. – MHNG-INVE-69655; Japan, Okinawa Islands, SE of Kume Island, 26.2776°N 126.89145°E, 151-160 m; 12.11.2009; fertile colony.

Diagnosis: *Zygophylax* species with pinnate colonies reaching 10 cm in height, stem may be branched, polysiphonic, hydrocladia usually monosiphonic, perisarc of stem and branches pale yellow. Hydrothecae campanulate, about 0.45 mm deep, pedicel and apophysis without distinct node separating them. Nematothecae variably present on apophyses of hydrothecae, short, tubular. Gonothecae densely packed in coppiniae and contiguous, bottle-shaped, widening from base onward, opening on a distinct neck (1/4 of total height), neck straight or curved, sometimes hood-like. No protective tubules. Large (30 µm) macrobasic euryteles present in polyps and coenosarc.

Description (Okinawa material): Colonies erect, pinnate (Fig. 8A), up to 7 cm; individual plume with distinct, straight stem bearing two rows of branches (hydrocladia) in one plane, all hydrothecae also in same plane. Perisarc of stem thick and firm, horny brown-yellow in colour, that of peripheral tubules much thinner.

Stem composed of axial tube and several parallel accessory tubes, all without distinct nodes. Two types of apophyses on axis, those bearing hydrocladia and others supporting axial hydrothecae. Stem apophyses supporting hydrocladia sub-opposite; two stem hydrothecae between each pair of hydrocladial apophyses, stem apophyses with

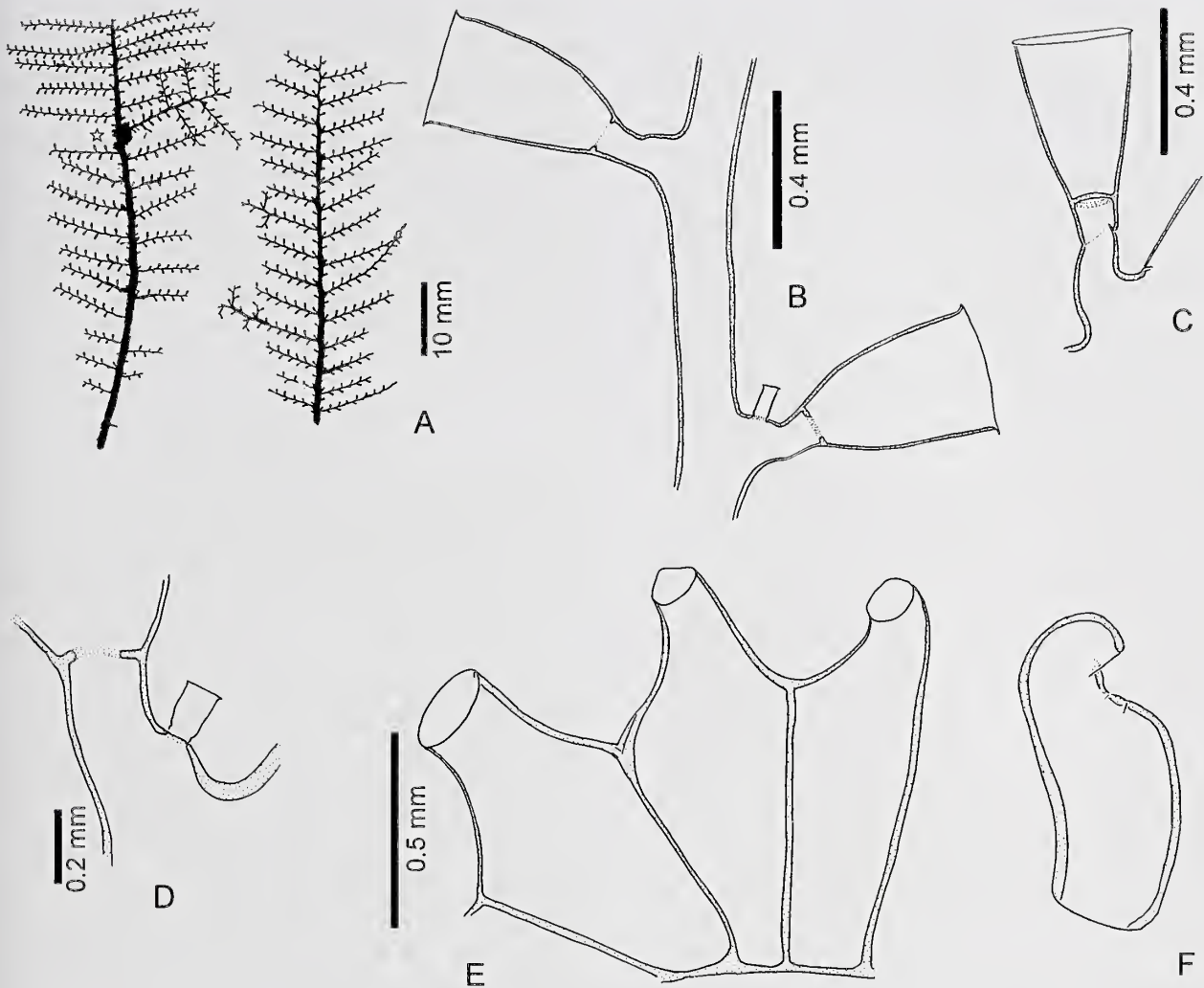


Fig. 8. *Zygophylax cyathifera*. (A) Silhouettes of two colonies, note the coppinia (star), MHNG-INVE-69626. (B) Two hydrothecae of hydrocladium, MHNG-INVE-69648. (C) Hydrotheca with indistinct node separating it from apophysis, MHNG-INVE-69655. (D) Apophysis with nematotheca and base of hydrotheca, MHNG-INVE-69655. (E) Optical section of part of coppinia showing three adnate gonothecae, MHNG-INVE-69655. (F) Isolated gonotheca with strongly curved neck part (opening), same scale as E, MHNG-INVE-69648.

axillary hydrotheca and 0-2 nematothecae (some lost during collection). Main axial tube and accessory tubes may occasionally bear nematothecae. Stem hydrothecae in two opposite rows, alternating in position.

Hydrocladia subopposite, up to 12 mm long, bearing up to 28 hydrothecae, mostly monosiphonic, occasionally with an auxiliary tube, occasionally hydrocladia branched (Fig. 8A). Hydrothecae of hydrocladia alternate, in two opposite rows, all in same plane.

Basal part of hydrotheca not separated from apophysis by distinct node or occasionally by indistinct one (Fig. 8C). Hydrotheca campanulate, nearly symmetrical, less than two times as long as wide, depth from diaphragm 0.45 mm, diaphragm with large, circular opening. Perisarc of hydrotheca firm, gradually thinning out along hydrothecal wall. Hydrothecal aperture circular, slightly

everted and often with 1-3 renovations. One nematotheca on most apophyses bearing the hydrothecae (Fig. 8B), often missing (lost?). Nematothecae small (Fig. 8D), cup-shaped, with circular, slightly everted rim and slightly bulging, almost parallel walls; perisarc very thin. Gonothecae aggregated into coppiniae encircling the stem (Fig. 8A), protective branches and nematothecae absent. Gonothecae tightly packed, adnate and lateral walls partially fused. Individual gonotheca bottle-shaped (Fig. 8E-F), with distally widening body turning into tubular neck with a terminal opening, neck about 1/4 of total height, straight or curved, occasionally even curved for more than 90° (Fig. 8F).

The hydranths and the coenosarc contain conspicuous, very large (30 µm) macrobasic euryteles, this in addition to the small nematocyst found on the tentacles.

Type localities: *Zygophylax cyathifera*, Vanuatu, Epi Island, 16.75°S 168.12°E 115-237 m (Allman, 1888). *Zygophylax pacifica*, Japan, Sagami Bay, Okinose Bank, 34.9535°N 139.2760°E, depth 250 m (Ruthensteiner *et al.*, 2008).

Distribution: Vanuatu Islands (Allman, 1888), Zanzibar and South Africa (Rees & Vervoort, 1987), Philippines (Vervoort, 1941, as *Z. pacifica*), Japan, from Sagami Bay to Okinawa Islands (Hirohito, 1995; this study).

Remarks: The present material fits very well the description of Stechow (1923c) and Hirohito (1995) for the Japanese *Z. pacifica*. However, there is nothing that would allow to separate this species reliably from *Z. cyathifera* (Allman, 1888) described by Rees & Vervoort (1987) using the type material of the species. The only difference is that in *Z. cyathifera* the basal part of hydrotheca is separated from the apophysis by a distinct node. While such a node is absent or at best indistinct in the present material, it is certainly not a character suitable for a species distinction. *Zygophylax pacifica* (Stechow, 1920) is therefore regarded as not distinguishable from *Z. cyathifera* and the former name becomes a junior synonym of the latter. The type material of *Z. cyathifera* was collected in the Vanuatu Islands (then New Hebrides), which is from a biogeographic point of view rather close to the type locality of *Z. pacifica* (Sagami Bay, Japan).

Zygophylax cyathifera resembles very much *Z. biarmata* (Ramil & Vervoort, 1992a), but the latter has often two nematothecae at the base of the hydrothecae and, more importantly, the coppiniae have protective tubules and the gonothecae are not adnate. As already pointed out by Ramil & Vervoort (1992a), the Japanese material

identified by Hirohito (1983, 1995) as *Z. biarmata* unlikely belongs to this species as the gonothecae have 2-3 long, horizontal horn-like processes. The same is also true for the Korean *Z. biarmata* described by Park (2010). This Pacific *Zygophylax* material belongs likely a yet unnamed species.

Zygophylax rufa (Bale, 1884) is also deceptively similar to *Z. cyathifera*, but has characteristically red colonies, the necks of the gonothecae are always strongly recurved and look hood-like, and there are nematothecae at the bases of the gonothecae (Fig. 9D).

Zygophylax rufa (Bale, 1884)

Fig. 9A-D

Campanularia rufa Bale, 1884: 54, pl. 1 fig. 1.

Lictorella rufa. – in part Vervoort & Vasseur, 1977: 15, figs 5-8.

– Gibbons & Ryland, 1989: 395: fig. 15.

Zygophylax rufa. – Rees & Vervoort, 1987: 55. – Schuchert, 2003: 159, fig. 18.

? *Zygophylax antipathes*. – Hirohito, 1983: 24, fig. 7. [not *Zygophylax antipathes* (Lamarck, 1816)]

Material: MHNG-INVE-60995; Japan, Okinawa Island, Mizugama 26.35897°N 127.7386°E, 4 m; 13.05.2008; three pinnate stems including hydrorhiza, up to 4 cm high, one stem with aggregated female gonothecae, each containing one egg/embryo.

Diagnosis: *Zygophylax* species with stem and branches reddish-purple to mahogany coloured, stem polysiphonic, not much branched, hydrocladia pinnately arranged and not around the stem, more or less alternate. Hydrotheca campanulate, about 0.3-0.4 mm deep, pedicel with or without node. Nematothecae

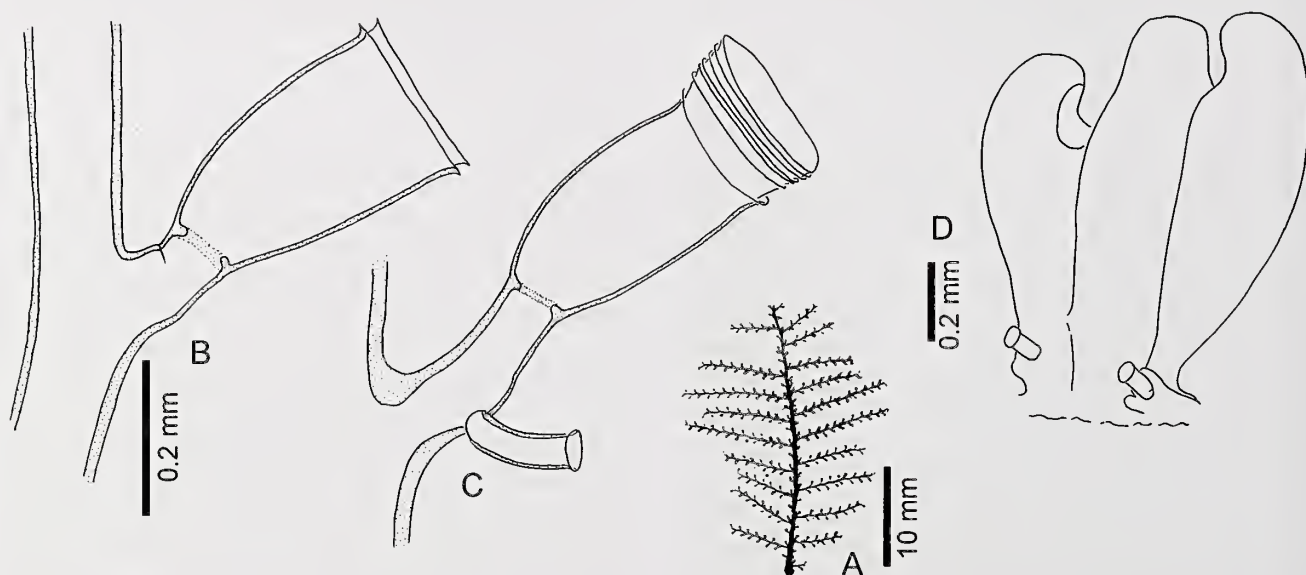


Fig. 9. *Zygophylax rufa*, MHNG-INVE-60995. (A) Silhouette of a stem. (B-C) Hydrothecae, note renovations of rim and nematotheca on pedicel of hydrotheca at right. (D) Group of three gonothecae, note nematothecae at base.

infrequent, on pedicels/apophyses of hydrothecae, tubular. Gonothecae in coppinae, densely packed and contiguous, slightly widening from base onward, near apex suddenly narrowed into hooded structure with rounded top, with lateral opening. Nematothecae are present at the bases of the gonothecae (Fig. 9D). One egg/embryo per gonotheca.

Description: See Vervoort & Vasseur (1977), Gibbons & Ryland (1989), or Schuchert (2003).

Type locality: Australia, Great Barrier Reef, Holborne Island (Bale, 1884).

Distribution: Great Barrier Reef, French Polynesia, Fiji Islands, Kei Islands, Okinawa Islands.

Remarks: *Zygophylax rufa* and *Z. antipathes* (Lamarck, 1816) are very similar (see discussions in Watson, 1973; Vervoort & Vasseur, 1977; Schuchert, 2003). The present material was identified as *Z. rufa* because it had pinnate stems with hydrocladia in one plane (Fig. 9A) and a purple perisarc.

The nematothecae at the base of the gonothecae have not been noted so far, but only few coppinae of this species have been described (Vervoort & Vasseur, 1977; Gibbons & Ryland, 1989).

This is the first record of this species for Japan, but the doubtful record of *Z. antipathes* by Hirohito (1983) may actually have been *Z. rufa* because the stem heights of 4 cm and the strictly pinnate hydrocladial arrangement are more characteristic for the latter species. See also the remarks under *Z. cyathifera*.

Zygophylax sibogae Billard, 1918

Fig. 10A-B

Zygophylax sibogae Billard, 1918: 21, fig. 1. – in part Totton, 1930: 167, fig. 21. – Ralph, 1958: 311, fig. 2e-i. – Millard, 1975: 198, fig. 65A-C. – Rees & Vervoort, 1987: 72. – Hirohito, 1995: 144, fig. 45a-d, pl. 9 fig. D. – Watson & Vervoort, 2001: 159, fig. 5a-d. – Vervoort & Watson, 2003: 80, figs 13G-K, 14A-B. – Schuchert, 2003: 160, fig. 19. – Vervoort, 2006: 247, fig. 19b-c.

Material: MHNG-INVE-69633; Japan, Okinawa Islands, N of Kume Island, 26.3932°N 126.7535°E, 95.5–123 m; 19.11.2009. – MHNG-INVE-69665; Japan, Okinawa Islands, W of Kume Island, 26.3283°N 126.71595°E, 93–101 m; 19.11.2009.

Diagnosis: *Zygophylax* with polysiphonic stem and branches, stem branching several times, hydrocladia alternate. Hydrotheca with long and slender pedicel (part below diaphragm), then widening, opening trumpet-shaped and held perpendicular to the axis of the lower part of hydrotheca (Fig. 10A), resulting in a deep fold on one side, hydrotheca total height 0.5–0.8 mm. Diaphragm well formed. Nematothecae tubular, at base of hydrocladia and on apophyses of hydrothecae, not always present. Gonothecae loosely aggregated in

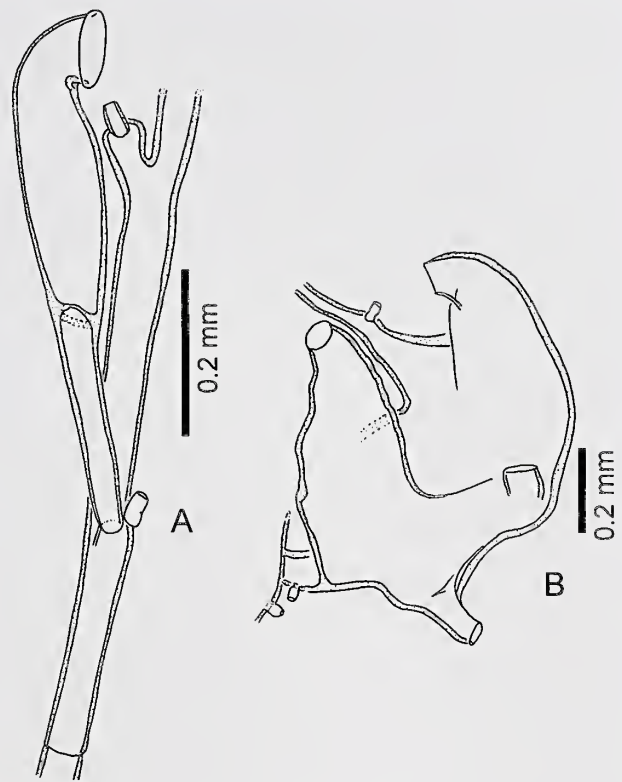


Fig. 10. *Zygophylax sibogae* MHNG-INVE-69633. (A) Part of hydrocladium with one hydrotheca. Note the presence of a small nematotheca on the apophysis. (B) Gonotheca, note irregular shape.

coppinia on stem, gonothecae not adnate, shape very irregular sac-shaped (Fig. 10B), with 1–3 openings on tubular extensions. Coppinia comprise also protective branches, branched, forming canopy over gonothecae, with nematothecae.

Description: See Hirohito (1995), Schuchert (2003), and Vervoort (2006).

Type locality: Indonesia, 5.667°S 132.433°E, 310 m (Rees & Vervoort, 1987).

Distribution: Indonesia, New Zealand, South Africa, Japan, Tasmania, Bay of Biscay to Cape Verde Islands (Vervoort, 2006).

Zygophylax tizardensis Kirkpatrick, 1890

Fig. 11A-B

Zygophylax tizardensis Kirkpatrick, 1890: 12, pl. 3 fig. 3. – Rees & Vervoort, 1987: 66. – Hirohito, 1995: 150, fig. 47a-d, pl. 10 fig. B. – Vervoort & Watson, 2003: 82, fig. 14C-E. – Peña Cantero, Marques & Migotto, 2004: 4, fig. 2C, synonymy.

Acryptolaria normani Nutting, 1927: 209, pl. 41 figs 1–2. – Peña Cantero, Marques & Migotto, 2004: 1, figs 1–2A–B, synonym.

Material: MHNG-INVE-69624; Japan, Okinawa Islands, S of Kume Island, 26.24542°N 126.81745°E, 141–165 m; 20.11.2009; fertile colony. – MHNG-INVE-69660; Japan, Okinawa Islands, NE of S of Kume Island, 26.38277°N 126.799°E, 81–82 m; 10.11.2009; sterile. – MHNG-INVE-69661; Japan, Okinawa Islands, SE of Kume Island, 26.27338°N 126.8581°E, 116 m; 11.11.2009; sterile. – MHNG-INVE-69667; Japan, Okinawa Islands, W of Kume Island, 26.3283°N 126.71595°E, 93–101 m; 19.11.2009; sterile.

Diagnosis: *Zygophylax* with polysiphonic stem and branches, stem not branched or a few times only, hydrocladia alternate. Hydrothecae (Fig. 11A) conical, distal 1/3 to 1/4 bent at right angle, pedicel (part below diaphragm) short, with internal, adcauline semi-circular ridge in about 2/3 of height. Coppinae almost spherical on stem or on branches, composed of relatively few gonothecae and many protective tubes bearing nematothecae (Fig. 11B), branching and anastomosing with each other, covering gonothecae like a canopy. Gonotheca sac-like, at distal end two or three horizontal, curved opening tubes, sometimes with a nematotheca near base (Fig. 11B).

Description: See Hirohito (1995) and Peña Cantero *et al.* (2004).

Type locality: Tizard Reef, Spratly Islands (Chinese Sea) (Kirkpatrick, 1890).

Distribution: Spratly Islands, Japan, Philippines, and New Zealand, 63–720 m.

Family Sertulariidae Lamouroux, 1812
Genus *Caminothujaria* von Campenhausen, 1896

***Caminothujaria molukkana* von Campenhausen, 1896**

Fig. 12

- Caminothujaria molukkana* von Campenhausen, 1896a: 106. – Vervoort, 1993: 102. – Schuchert, 2003: 182, fig. 38.
Caminothujaria moluccana. – von Campenhausen, 1896b: 306, 314, pl. 15 fig. 8. [incorrect spelling]
Thuiaria divergens Whitelegge, 1899: 372, pl. 23, figs 1–3. – Billard, 1925: 222, synonym.
Sertularia indomalayica Stechow, 1919: 158, new name for *Caminothujaria molukkana* von Campenhausen, 1896.
Sertularella singularis Billard, 1920: 14, fig. 1.
Sertularia sigmagonangia Hargitt, 1924: 495, pl. 5 fig. 20.
Sertularella moluccana. – Billard, 1925: 167, figs 28–29, pl. 7 fig. 19.

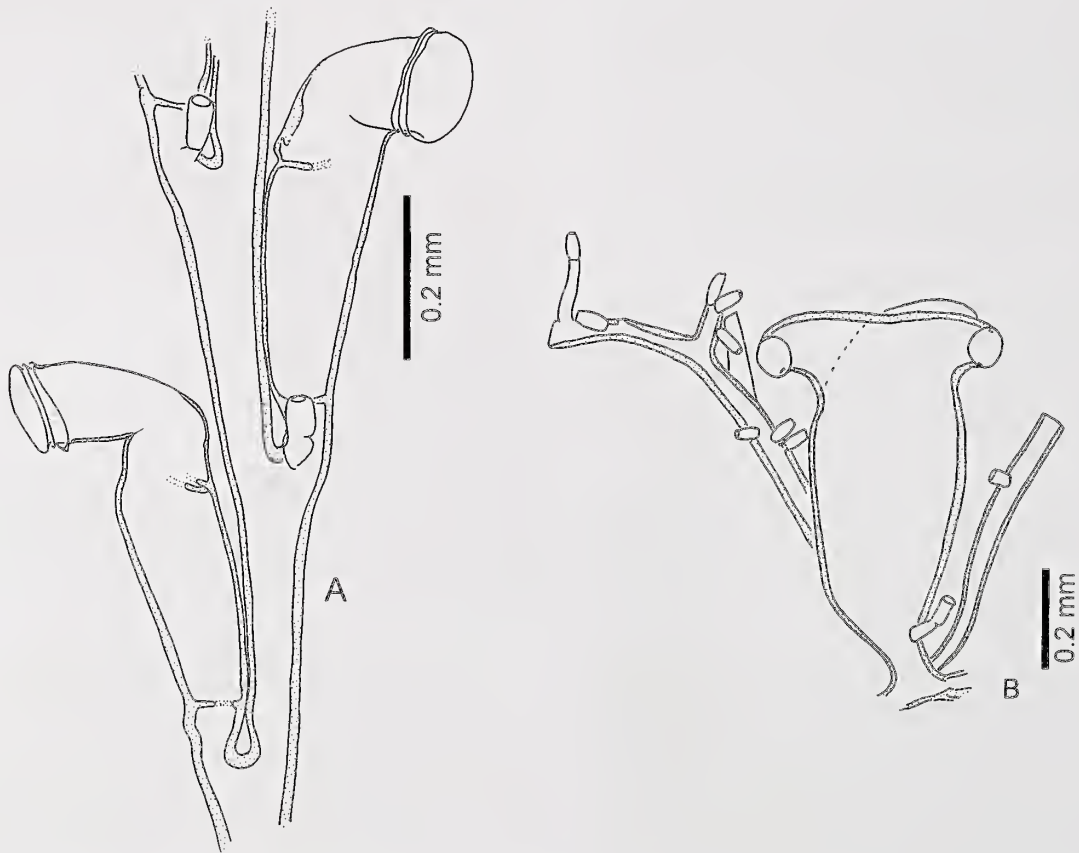


Fig. 11. *Zygophylax tizardensis*, MHNG-INVE-69624. (A) Two hydrothecae of branch, note presence or absence of nematotheca at pedicel base. (B) Gonotheca with protective tubules bearing nematothecae. Note also the single nematotheca at the base of the gonotheca.

Dictyocladium aberrans Nutting, 1927: 214, pl. 41 figs 4-5.

Tridentata funafutiensis Stechow, 1923a: 12, new name for *Thuiaria divergens* Whitelegge, 1899.

Material: MHNG-INVE-69636; Japan, Okinawa Islands, S of Kume Island, 26.2601°N 126.8234°E, 91-105 m; 20.11.2009; three plumes with gonothecae. – MHNG-INVE-69646; Japan, Okinawa Islands, SE of Kume Island, 26.30028°N 126.82563°E, 30-40 m; 11.11.2009; without gonothecae.

Diagnosis: Sertulariidae with pinnate, polysiphonic stems reaching heights of 7 cm. At least some hydrothecae of the hydrocladia arranged in whorls of four (two opposite pairs, Fig. 12), always also regions with paired hydrothecae or sometimes three hydrothecae per whorl.

Hydrotheca uniform, abcauline wall about 0.45 mm long, diameter of opening 0.22 mm; rim with four low but acute cusps; operculum composed of four valves, pyramid-like; renovations of margin and opercula frequent.

Gonothecae shape elongate fusiform and slightly S-like curved, about 2 mm long, maximal diameter 0.6 mm; with 6-8 transverse crests; opening terminal, surrounded by three distinct eusps, covered by operculum divided into four flaps.

Description: See Hirohito (1995).

Type locality: Ternate, Moluccas, Indonesia (von Campenhausen, 1896a).

Distribution: Indonesia, Funati Atoll, Philippines, Macclesfield Bank (Chinese Sea), Japan.

Remarks: This is the first record of this characteristic tropical species for Japan, which was otherwise only known to occur from Indonesia to the Philippines. It

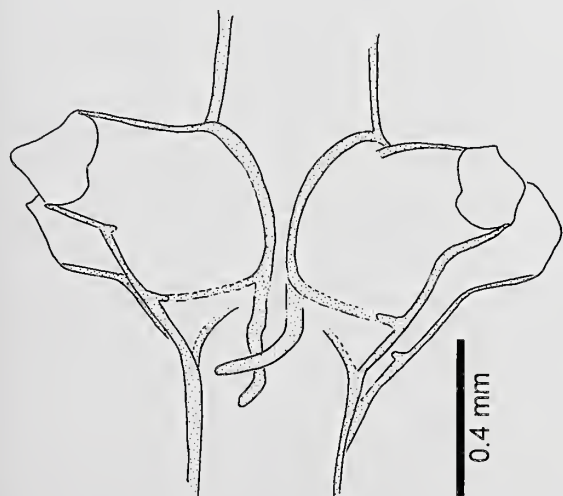


Fig. 12. *Caminothujaria molukkana*, MHNG-INVE-69636, whorl of four hydrothecae from hydrocladium.

was noted that 2-3 finger-like processes arise from the bottoms of the hydrothecae (Fig. 12). These processes were also observed in material from the Kei Islands (Schuchert, 2003).

Genus *Sertularella* Gray, 1848

Sertularella mirabilis Jäderholm, 1896

Fig. 13

Sertularella mirabilis Jäderholm, 1896: 9, pl. 2 fig. 1. – Nutting, 1927: 216, pl. 42 figs 3-4. – Hirohito, 1995: 195, fig. 64a-g, pl. 12 fig. B. – Park, 2010: 96, fig. 53.

Material: MHNG-INVE-69650; Japan, Okinawa Islands, SE of Kume Island, 26.2624°N 126.857°E, 150-168 m; 12.11.2009, without gonothecae.

Diagnosis: *Sertularella* species with colony developing into a three-dimensional lattice, resembling a sponge, size up to 10 cm. Hydrothecae typical for genus, usually with several transverse ridges, somewhat variable. Gonotheca ovoid, opening on terminal neck, main body usually with transverse sculptures.

Description: See Hirohito (1995).

Type locality: Japan, off Hirado, 33.167°N 129.300°E, 82 m depth (Jäderholm, 1896).

Distribution: South China Sea, Japan, Korea.

Remarks: The unique, three-dimensional structure resembling a sponge (Fig. 13A) makes this species rather easy to identify.

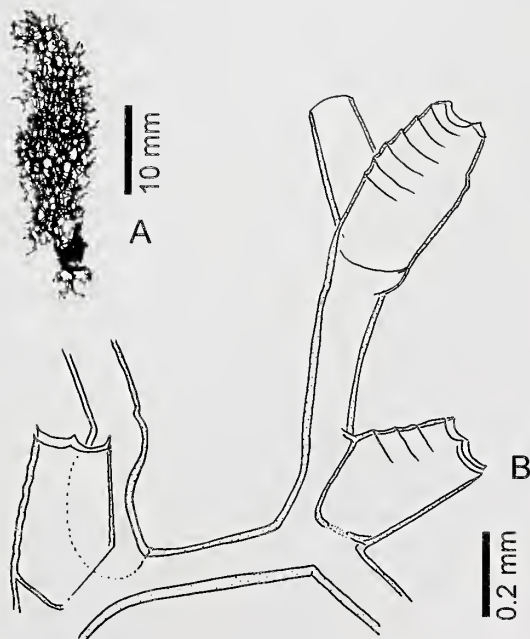


Fig. 13. *Sertularella mirabilis*, MHNG-INVE-69650. (A) Colony silhouette. (B) Hydrothecae.

Family Thyroscyphidae Stechow, 1920
Genus *Thyroscyphus* Allman, 1877

***Thyroscyphus fruticosus* (Esper, 1797)**

Fig. 14

Sertularia fruticosa Esper, 1797: plate 34.

Sertularia laxa Lamarck, 1816: 116. (new name for Esper's material)

Laomedea fruticosa. – Hammer in Esper, 1829: 162.

Thyroscyphus vitiensis Marktanner-Turneretscher, 1890: 210, pl. 3 fig. 4. – Gibbons & Ryland, 1989: 427, synonym.

? *Campanularia thyroscyphiformis* Marktanner-Turneretscher, 1890: 206, pl. 3 fig. 4. – Rees & Vervoort, 1987: 67.

Campanularia juncea Allman, 1876: 260, pl. 11 fig. 3-4.

Thyroscyphus fruticosus. – Spletstösser, 1929: 7, figs 1-11, 13-27. – Ralph, 1961: 754, fig. 1a. – Vervoort, 1967: 35, figs 8-9. – Millard, 1975: 323, fig. 104. – Gibbons & Ryland, 1989: 425, fig. 40. – Watson, 2000: 38, fig. 29D. – Schuchert, 2003: 195, fig. 49.

Material: MHNG-INVE-91095; Japan, Okinawa Island, off Ada village, depth 7 m; 21.06.2008; two fertile colonies.

Diagnosis: Indo-Pacific *Thyroscyphus* with erect, flat, pinnately branched colonies, rose-pink in life, 5-20 cm, stem stiff, monosiphonic, nodes absent or indistinct. Hydrocladia alternate, nodes indistinct or absent. Hydrotheca campanulate, wall smooth, 1-1.2 mm deep, diameter at opening 0.5-0.6 mm, slightly bilateral symmetric through bulging upper side and almost straight underside, at base a distinct diaphragm, margin mostly smooth, occasionally with four indistinct, shallow cusps. Operculum four triangular flaps, usually lost and only present in very young hydrothecae. Gonothecae on stem and hydrocladia, developing on apophyses of hydrothecae, about 2 mm long, oblong oval, basal part tapering, end truncated, wall smooth.

Description: See Schuchert (2003).

Type locality: Indian Ocean (Esper, 1829).

Distribution: Tropical Indo-West Pacific, Japan, New Zealand, southern and western Africa, Mediterranean (Schuchert, 2003).

Remarks: This species was named by Esper (1788-1830) in a work which appeared in numerous issues, the text and plates usually at very different dates. His figures, labelled *Sertularia fruticosa*, permit to recognise the species unambiguously. The publication date of this plate has only become known through the investigations of Grasshoff & Scheer (1991). According to the latter publication, the plate 34 with *S. fruticosa* was published in 1797. Lamarck (1816) named Esper's hydroid *Sertularia laxa*, which must now be taken as an objective synonym. The text for Esper's plate was only published 19 years after Esper's death in 1829 by H. L. Hammer under the name *Laomedea fruticosa* [note, the genus *Laomedea* was introduced by Lamouroux (1812), so it was not known to Esper].

Thyroscyphus fruticosus is a common and widespread hydroid in the tropical Indian- and western Pacific Ocean. It's occurrence in Japanese waters is here documented for the first time.

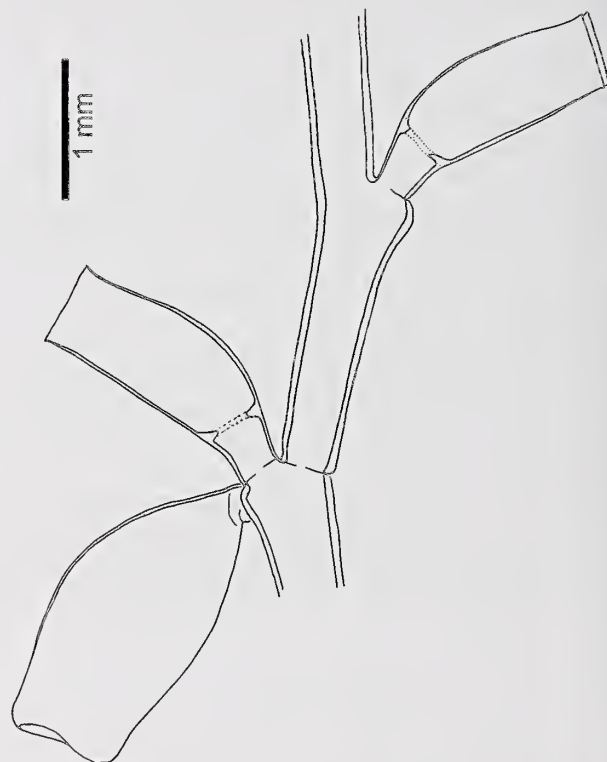


Fig. 14. *Thyroscyphus fruticosus* MHNG-INVE-91095, part of hydrocladium with two hydrothecae and a gonotheca (lower left).

Family Haleciidae Hincks, 1868
Genus *Hydrodendron* Hincks, 1874

***Hydrodendron stechowii* Hirohito, 1995**

Fig. 15

Ophioides arboreus. – Stechow, 1913: 87. – Jäderholm, 1919: 6, pl. 1 fig. 6. [not *Hydrodendron arboreum* (Allman, 1888)]

Hydrodendron (Dendrophiodissa) stechowii Hirohito, 1995: 32, fig. 9a-c, pl. 2 fig. 2.

Material: MHNG-INVE-69647; Japan, Okinawa Islands, SE of Kume Island, 26.2624°N 126.857°E, 150-168 m; 12.11.2009; 1 colony 7 cm without gonothecae.

Diagnosis: Colonies up to 18 cm high, stem polysiphonic and branching, Hydrocladia monosiphonic, pinnately arranged in two rows, opposite or subopposite. Hydrocladia subdivided by transverse nodes delimiting segments of variable length. Each segment with a hydrotheca near its distal end, alternating

sides and thus in two rows. Hydrotheca on short hydrophore, adcauline side of hydrophore very short or non-existent, hydrotheca thus sessile. Hydrotheca 0.2 mm in diameter and very short (about 20 μ m high), inclined about 45° towards below, walls straight, on inside a number of thick desmocytes. On about ever second to third segment a nematotheca, located close to proximal end of segment on side opposite of hydrotheca. Nematothecae similar to hydrotheca but smaller (about 1/3), a short, somewhat conical collar surrounding a hole in the segment. On inside of nematotheca a number of thick desmocytes. Gonothecae loosely aggregated in a scapus attached to the stem. Scapus consist of tangled mass of tubes bearing paired gonothecae. Gonothecae flask-shaped, opening in a distal neck which is not recurved (after Hirohito, 1995).

Description: See Hirohito (1995).

Type locality: Japan, Honshu Island, Sagami Bay, Okinose Bank (Hirohito, 1995).

Distribution: Japan only; Sagami Bay (Steehow, 1913; Hirohito, 1995), Goto Islands (Jäderholm, 1919), Okinawa Islands (this study). Depth range from 30 to 200 m.

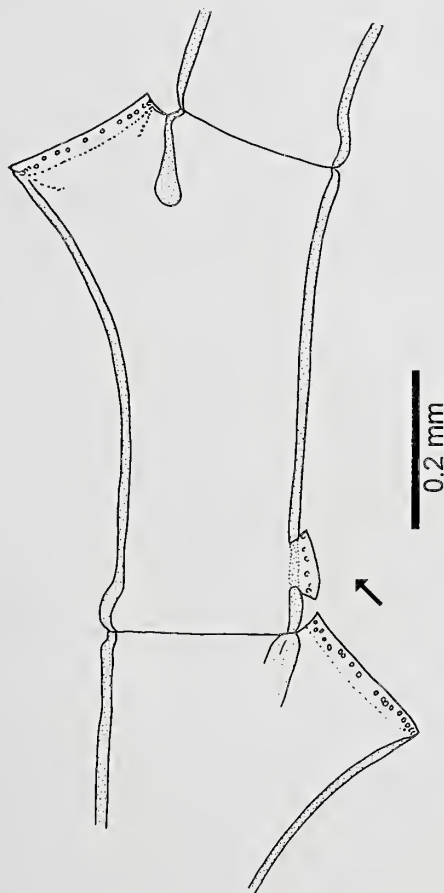


Fig. 15. *Hyrodendron stechowi*, MHNG-INVE-69647, hydrocladial segment with a nematotheca near its base (arrow).

Remarks: This species resembles *H. arboreum* (Allman, 1888) and *H. tottoni* Rees & Vervoort, 1987. These two species have gonothecae with recurved necks. Moreover, the nematothecae are smaller and the position appears to move towards the middle of the segment (see Ralph, 1958; Peña Cantero & Ramil, 2006).

Hyrodendron leloupi Hirohito, 1983

Fig. 16A-B

Diplocyathus dichotomus. – Leloup, 1938: 5, fig. 2. [not *Diplocyathus dichotomus* Allman, 1888]

Hyrodendron leloupi Hirohito, 1983: 13, fig. 2.

Hyrodendron (Hyrodendron) leloupi. – Hirohito, 1995: 34, fig. 9d-j, pl. 2 fig. D.

? *Phylactotheca pacifica* Stechow, 1913: 155, fig. 135.

Material: MHNG-INVE-69631; Japan, Okinawa Islands, N of Kume Island, 26.39317°N 126.7535°E, 95.5-123 m; 19.11.2009; several stems, up to 5 cm, one with 2 presumed gonothecae. – MHNG-INVE-69651; Japan, Okinawa Islands, SE of Kume Island, 26.2624°N 126.857°E, 150-168 m; 12.11.2009; 7 cm stem, no gonothecae, few nematothecae.

Diagnosis: Colonies 3-10 cm, mono- or polysiphonic stem, branched or not, hydrocladia more or less pinnately arranged, monosiphonic, with oblique or transverse nodes, nodes irregular and internodes of different length and with differing numbers of hydrothecae. Hydrothecae in two rows, alternating sides, on short apophyses of hydrocladia, about 0.3 mm long, deep, trumpet-shaped, margin smooth and slightly everted. On inside of hydrotheca an irregular circle of refringent dots, diaphragm extremely thin and inconspicuous (often invisible), oblique. Nematothecae goblet-shaped, about 70 μ m, placed mostly immediately distal to apophyses, but also on apophyses possible, not all apophyses have nematothecae, sometimes they can be rare. Gonothecae up to 0.9 mm high and half as wide, on basal part of stem or stolons, not aggregated, conical when young, mature cylindrical. Larviparous.

Description: See Hirohito (1983, 1995).

Type locality: Japan, Bonin Islands (Hirohito, 1983).

Distribution: Japan.

Remarks: The stem heights in Hirohito (1983, 1995) are given incorrectly in mm instead of cm.

This species is very unlike *Halecium* and rather reminiscent of *Zygophylax* (Lafocidae). Molecular data are needed to corroborate the correct genus allocation.

In the present material, only one stem had two structures that could be gonothecae (Fig. 16B). They were conical, with some transverse creases. They are thus unlike the smooth, cylindrical gonothecae depicted in Hirohito (1995). Because these thecae were empty, only about half

the size as given by Hirohito, and partially damaged, they are perhaps only aborted growth-stages of basal parts of normal gonothecae.

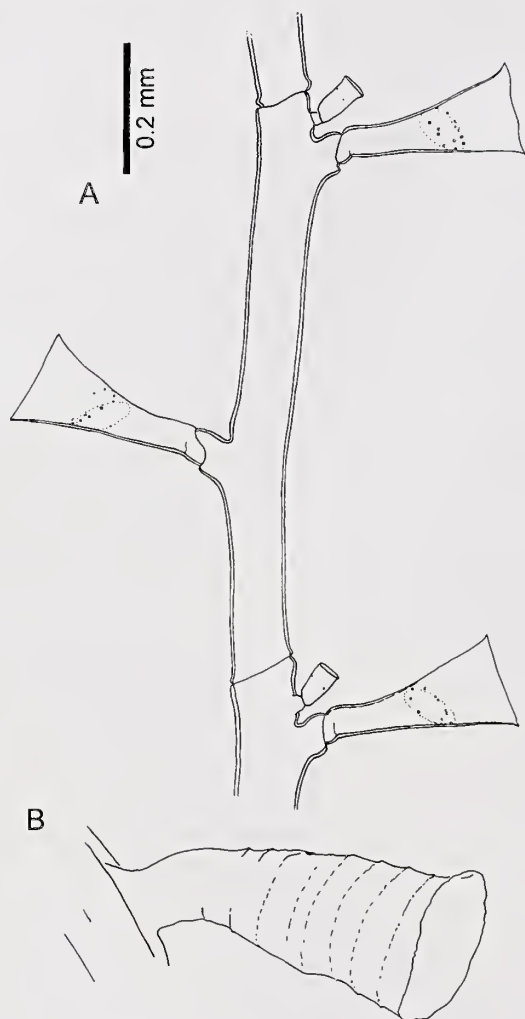


Fig. 16. *Hydrodendron leloupi*, MHNG-INVE-69651. (A) Part of hydrocladium. Note the two nematothecae distal to the apophyses. (B) Presumed gonotheca or part of a gonotheca; same scale as A.

Family Halopterididae Millard, 1962
Genus *Antennella* Allman, 1877

***Antennella quadriaurita* Ritchie, 1909**
 Fig. 17A-C

Antennella quadriaurita Ritchie, 1909: 92, fig. 9. – Millard, 1977: 123, fig. 8. – Schuchert, 1997: 29, fig. 9. – Vervoort & Watson, 2003: 344, fig. 83F-I. – Galea, 2010: 11, fig. 4s.

Antennella quadriaurita forma *africana* Broch, 1914: 26.

Antennella africana. – Ralph, 1961: 23, figs 1a-c, f-g. – Millard, 1975: 331, fig. 107A-E.

Antennella serrata Totton, 1930: 212, fig. 53. – Ralph, 1961: 25.

Antennella paucinoda Fraser, 1935: 110, pl. 2 fig. 10. – Hirohito, 1995: 235, fig. 78d-g.

Antennella variabilis Fraser, 1936: 52, fig. 6a-c.

Material: MHNG-INVE-69641; Japan, Okinawa Islands, SE of Kume Island, 26.2836°N 126.90072°E, 142-149 m; 13.11.2009; with gonothecae. – MHNG-INVE-69657; Japan, Okinawa Islands, W of Kume Island, 26.3474°N 126.6886°E, 96-186 m; 19.11.2009; with gonothecae; hydrotheca diameter 0.25-0.26 mm, abcauline wall 0.25-0.29 mm, stem diameter 0.12-0.14 mm, stem height up to 38 mm.

Diagnosis: *Antennella* species, stems up to 4 cm, with two pairs of lateral nematothecae (2 x 2), the more adcauline pair usually slightly smaller. One median inferior nematotheca well below hydrotheca. Intersegments with no hydrotheca delimited by distal

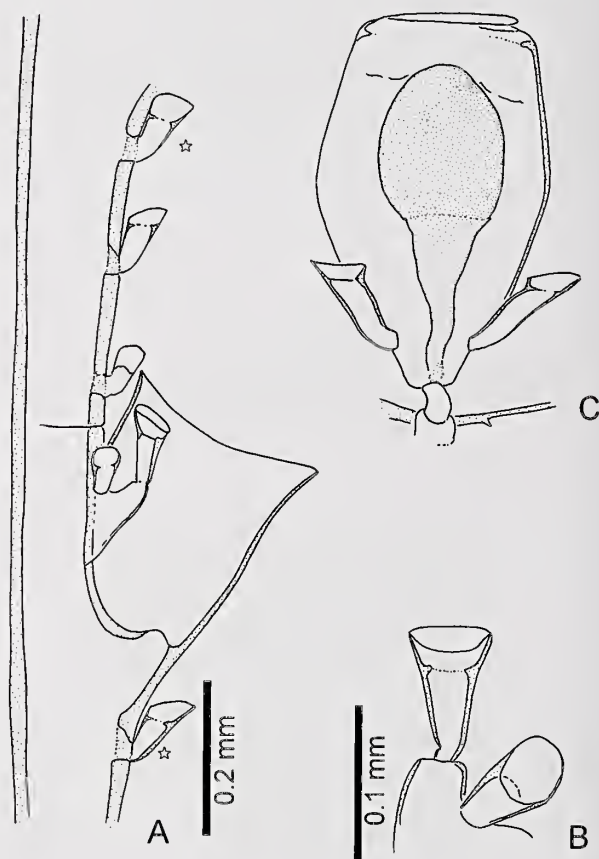


Fig. 17. *Antennella quadriaurita*, MHNG-INVE-69657. (A) Lateral view of stem with a hydrotheca. As typical for the samples examined here, the oblique nodes below the median inferior nematothecae are not visible. The transverse nodes above the hydrothecae are distinct, but weak too. Two homologues of median inferior nematothecae are marked with stars. (B) Pair of lateral nematothecae seen from adcauline side. (C) Gonotheca with soft tissue indicated, interpreted as female, same scale as A. The axis of the stem is horizontal in this figure.

oblique and proximal transverse node. Intersegments with 1-4 median nematothecae. Either the transverse or the oblique nodes can be weak or absent. Hydrotheca cylindrical, margin may be somewhat everted, adcauline side free for about 1/2 of length. Gonothecae of both sexes on same stem or not. Female gonothecae larger, two nematothecae at base, obtuse distal end with flat lid; male smaller, one nematotheca near base.

Description: See Schuchert (1997).

Type locality: Gough Island, South Atlantic; 183 m (Ritchie, 1909).

Distribution: Bermuda; Cuba; Tristan da Cunha Islands group; tropical west Africa; Vema Seamount; South Africa; India; New Zealand, Japan; Korea (Schuchert, 1997; Vervoort & Watson, 2003; Galea, 2010).

Remarks: The present material matched other material of this species described in Schuchert (1997), except for the oblique nodes which were mostly weak or entirely reduced. Some few, deep oblique nodes were, however, always present in an individual stem. This morphotype with reduced oblique nodes is so far only known from Japan and it has been described as a distinct species *Antennella paucinoda* Fraser, 1935. Hirohito (1995) redescribed *A. paucinoda*, but acknowledges its close similarity to *A. quadriaurita*. The latter is currently seen as a rather variable species (Schuchert, 1997) and within its broad scope, solely the reduction of the oblique nodes cannot be considered as sufficient to maintain *A. paucinoda* as a separate species. Because it has pairs of lateral nematothecae and no median one behind the hydrotheca it cannot be regarded as conspecific with *A. secundaria* as thought by Leloup (1938) and later uncritically reiterated by Schuchert (1997).

Family Schizotrichidae Peña Cantero, Sentandreu & Latorre, 2010

Genus *Schizotricha* Allman, 1883

Schizotricha longinema new. spec.

Fig. 18A-G

Holotype: MHNG-INVE-69653; Japan, Okinawa Islands, SE of Kume Island, 26.2776°N 126.89145°E, 151-160 m; 12.11.2009; without gonothecae, one plume, slide and alcohol material, hydrocladia unbranched.

Paratypes: MHNG-INVE-89083; Japan, Okinawa Islands, SE of Kume Island, 26.2776°N 126.89145°E, 151-160 m; 12.11.2009; one plume in alcohol, branched hydrocladia. – MHNG-INVE-89084; Japan, Okinawa Islands, SE of Kume Island, 26.2624°N 126.857°E, 150-168 m; 12.11.2009; in alcohol, one plume with gonothecae, with branched hydrocladia.

Diagnosis: *Schizotricha* species with polysiphonic stem,

up to 5 cm; the nematotheca immediately proximal of the hydrocladial hydrothecae (median inferior) exceptionally long, reaching 0.5 mm in size, movable. Other nematothecae large, but sizes fall within usual range. Gonothecae small, arising just proximal of long nematothecae, without nematothecae. Adcauline wall of hydrotheca completely adnate, hydrothecae rather shallow, as wide as deep, walls may be thickened.

Etymology: The specific epithet is derived from “long” and “nematotheca”.

Type locality: Japan, Okinawa Islands, SE of Kume Island, 26.2776°N 126.89145°E, 151-160 m.

Description: Pinnate colonies, up to 5 cm, arising from hydrorhiza formed by a tangled mass of stolons. Stem straight, unbranched, polysiphonic except for distal end, composed of a bundle of auxiliary tubed and a central main tube. Auxiliary tubes unsegmented, with movable nematothecae. Main tube with occasional transverse nodes only, with alternately arranged, long apophyses on which the hydrocladia are attached (Fig. 18C). In the upper axil of each apophysis a hydrotheca (Fig. 18B), slightly more shallow than the hydrocladial ones. Associated with each cauline hydrotheca are two lateral nematothecae, these much larger than hydrotheca, movable, the one on the side of the apophysis somewhat displaced behind the hydrotheca and directed away from it, hence often difficult to see. One more nematotheca on apophysis, at least one more nematotheca below apophysis on opposite side of the latter.

Hydrocladia thin and flexible, branched or not, if branched then bifurcation at level of first hydrotheca, total length up to 12 mm with up to 17 hydrothecae. First segment of hydrocladium short, without nematotheca. Rest of hydrocladium with irregularly occurring transverse nodes so that there are 1-3 hydrothecae per internode. No internal ribs. Hydrotheca rather shallow, about as wide as deep, cylindrical or cup-shaped, adcauline wall completely adnate, opening perpendicular to hydrocladium axis. Some hydrothecae may have very thick walls (Fig. 18F). Associated with each hydrotheca are the three usual nematothecae, a pair of laterals and a median inferior nematotheca. The median inferior nematotheca extraordinarily long (0.5 mm), usually straight, movable, two chambered, upper chamber large. All median inferior nematothecae of hydrocladium are of this length. The two lateral nematothecae as all others conical, movable, two-chambered, in comparison to hydrotheca relatively large, adcauline side slightly lowered. In addition to these three nematothecae about three median nematothecae between each pair of hydrothecae (Fig. 18D).

Gonothecae develop on hydrocladium immediately proximal of long median inferior nematothecae, up to 0.2 mm long, pear-shaped, without nematothecae.

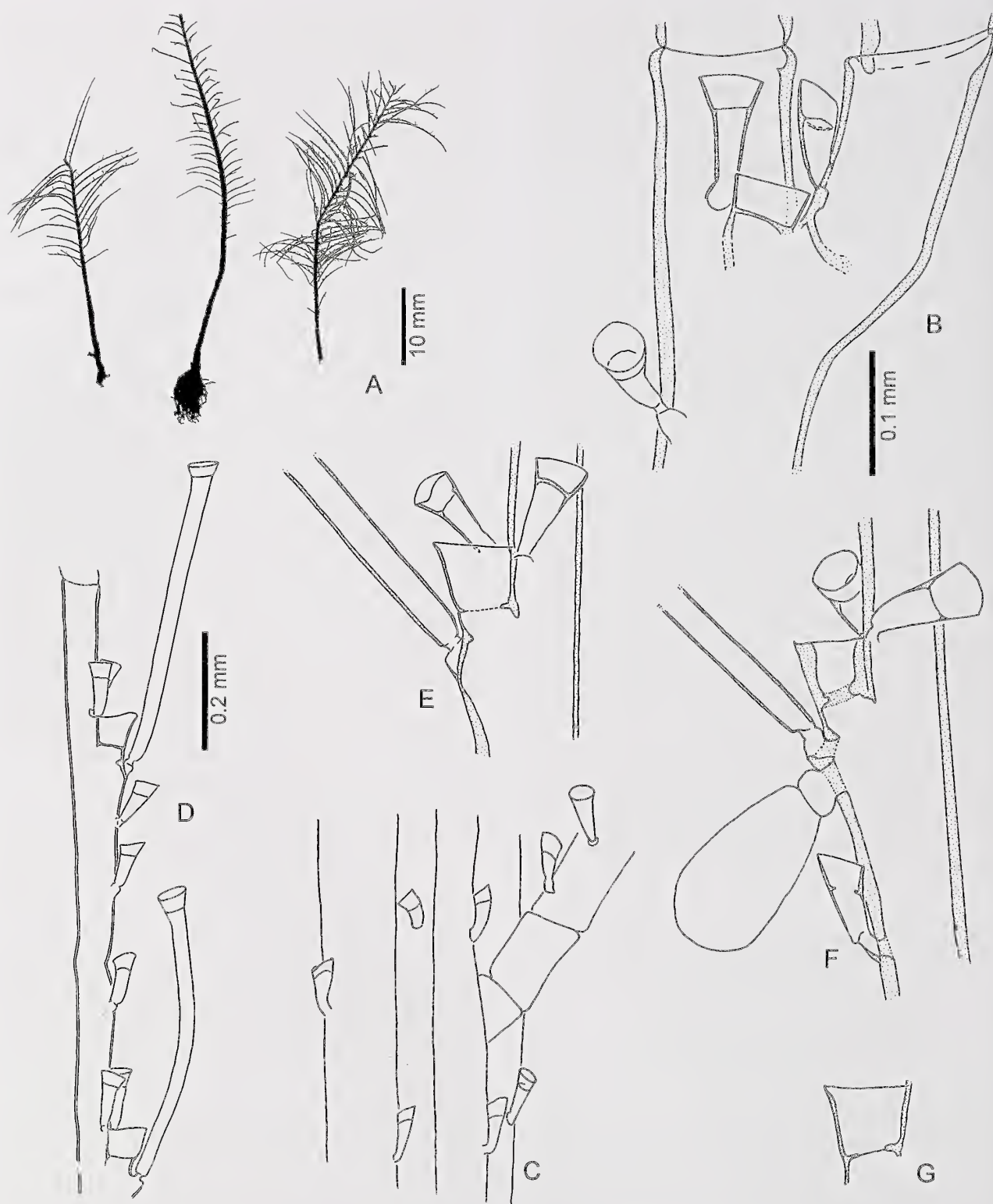


Fig. 18. *Schiztricha longinema* new spec., B-E holotype, F-G paratype. (A) Colony silhouettes, from left: holotype, paratype MHNG-INVE-89083, paratype MHNG-INVE-89084. (B) Main tube of stem in monosiphonic part showing at right an apophysis and a hydrotheca in its axil. Note that the right lateral nematothecae associated with the hydrotheca is not shown. It is usually displaced somewhat to the rear of the hydrotheca and difficult to observe. The nematotheca on the apophysis is an additional one, not the lateral one. (C) Stem in basal, polysiphonic part, showing auxiliary tubes bearing nematothecae and the base of a hydrocladium coming from the hidden main tube (same scale as D). (D) Part of hydrocladium with two hydrothecae. Note the characteristic, extremely long median inferior nematothecae. (E) Hydrotheca and its associated nematothecae, median inferior nematotheca only shown partially. Same scale as B. (F) Like E, but with gonotheca. Note the thickened hydrothecal wall. Same scale as B. (G) Hydrotheca of same branch as F but more distal, the hydrothecal wall is not thickened. Same scale as B.

Dimensions:

Plume heights: 3.5–5 cm

Main tube diameter: 0.11 mm

Apophyses: 0.2 mm

Hydrotheca of branches, abcauline wall: 50–55 μm

Hydrotheca diameter: 50–60 μm

Hydrocladium diameter: 40–105 μm

Median inferior nematotheca length: 0.5–0.56 mm

Lateral nematothecae on branches: 80–95 μm

Distribution: Okinawa Islands.

Remarks: All species of the genus *Schizotricha* have been reviewed by Peña Cantero & Vervoort (1999). Based on 16S gene sequence data, Peña Cantero *et al.* (2010) separated the genus from the Halopterididae and placed it in its own family Schizotrichidae.

The new species described here is unique among its congeners and immediately recognisable due to its very long median inferior nematotheca (Fig. 18D), which are about ten times the size of the hydrotheca. They are of a very exceptional length and no comparable case within the Plumularoidea is known. If not lost due to the collecting process, all median inferior nematothecae were of this size, this in all three specimens from two different localities. The length is thus not just a developmental aberration. Somewhat unusual for the genus, the gonothecae lacked nematothecae. Perhaps this is related to the hypertrophied adjacent median inferior nematotheca. It was not possible to identify reliably the sex of the gonothecae in the present sample, but they were more likely female.

Family Plumulariidae Agassiz, 1862

Genus *Nemertesia* Lamouroux, 1812

***Nemertesia octoseriata* (Jäderholm, 1896)**

Fig. 19A–E

Antennularia octoseriata Jäderholm, 1896: 15, pl. 2 fig. 6.

Antennularia dendritica Stechow, 1908: 195.

Antennularia Perrieri. – Stechow, 1909: 81. [not *Nemertesia perrieri* (Billard, 1901)]

Nemertesia irregularis. – Jäderholm, 1919: 23 pl. 5 fig. 7. [not *Antennularia irregularis* Quelch, 1885 = *Nemertesia antennina* (Linnaeus, 1758)]

Nemertesia antennina. – Hirohito, 1983: 66, fig. 34a–b. – Hirohito, 1995: 264, fig. 89a–g. – Park, 2010: 140, fig. 78A–E. [not *Nemertesia antennina* (Linnaeus, 1758)]

Type material: UZM specimen number UPSZ-TY2136; holotype of *Nemertesia octoseriata* Jäderholm, 1896; Japan, Hirado Strait, 33°5′–33°15′N 129°15′–129°16′E, 44 fathom (80 m); one sterile colony in alcohol. – ZSM 20051190, 20051186, and 20051194; 3 slides made by Stechow from holotype of *Antennularia dendritica* Stechow, 1908, Japan, Sagami Bay.

Non-type material: MHNG-INVE-69619; Japan, Okinawa Islands, S of Kume Island, 26.2466°N

126.8162°E, 123–153 m; 20.11.2009; sterile colony. – MHNG-INVE-69620; Japan, Okinawa Islands, S of Kume Island, 26.2545°N 126.7946°E, 114–115 m; 13.11.2009; sterile colony. – MHNG-INVE-69637; Japan, Okinawa Islands, S of Kume Island, 26.2601°N 126.8234°E, 91–105 m; 20.11.2009; sterile colony. – MHNG-INVE-89122; Japan, Okinawa Islands, SE of Kume Island, 26.2624°N 126.857°E, 150–168 m; 12.11.2009; colony with gonothecae.

Diagnosis: Colonies 4–13 cm high, stems unbranched, bases bundled and overgrown with stolon-like tubes thus giving polysiphonic appearance. Hydrocladia arranged in whorls, 2 to 5 hydrocladia per whorl, most frequently 2–4, adjacent whorls decussate, resulting in hydrocladia issuing in all directions from stem. Apophyses with 1–3 nematothecae. First segment of hydrocladium always lacking a hydrotheca, with one nematotheca in proximal region, rest of stem heteromerously segmented with main- and intersegments, nodes distinct. Main segments with hydrotheca in middle and the typical three nematothecae, median one not reaching to level of hydrotheca. Adauline side of hydrotheca completely adnate. Intersegments elongate, shorter or as long as main segments, with 1 to 2 nematothecae, usually either 1 or 2 in the whole colony and not so much variable within a colony. Gonothecae in axils of apophyses of stem, pear shaped, opening terminal, at right angle to long axis.

Description (Okinawa material): Colonies 4–8 cm high when mature, arising from a tuft of root-like, tubular stolons. Base of colony about 1–2 cm, composed of several stems and overgrown with stolon-like tubules, appearing thus tree-like with polysiphonic trunk (Fig. 19A). Stems above trunk-region free, irregular, unbranched, monosiphonic, with canaliculate coenosarc, perisarc nodes sparse. Hydrocladia arranged in whorls, predominantly one opposite pair per whorl (Fig. 19B), adjacent whorls decussate, resulting in hydrocladia issuing in all directions from stem. This pairwise arrangement occasionally in some parts replaced by 3–4 hydrocladia per whorl, or hydrocladia singly and irregularly arranged. Younger stems may have a true pinnate arrangement of hydrocladia as they are in two lateral rows only (not decussate).

Hydrocladia arise on long apophyses of stem, hydrocladia thin and relatively short (5 mm). Apophyses with 1–3 nematothecae in upper axil. Hydrocladia with distinct, first segment without hydrotheca and one nematotheca (if not lost), this segment always present. Remainder of hydrocladium heteromerously segmented by tandem repeats of main- and intersegments (Fig. 19C), 4–7 repeats per hydrocladium. Main segment with hydrotheca in lower third, almost entirely adnate, walls straight, not much thickened, opening tilted. One median inferior nematotheca and a pair of lateral nematothecae.

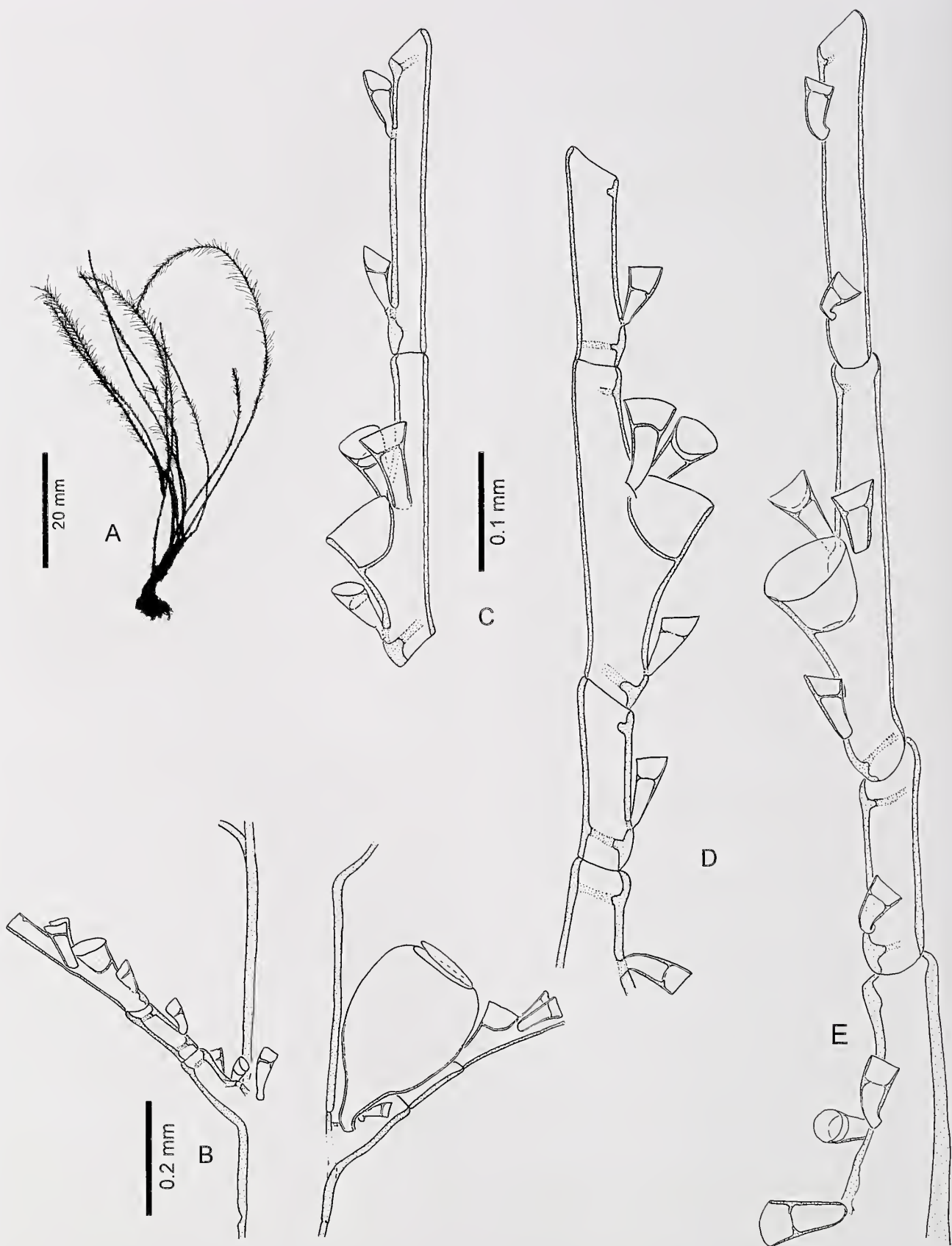


Fig. 19. *Nemertesia octoseriata*. (A) Colony silhouette, MHNG-INVE-69639. (B) Part of stem with hydrocladia and a gonotheca on apophysis, MHNG-INVE-89122. (C) Main- and intersegment of hydrocladium, MHNG-INVE-89122. (D) Apophysis, first segment, main- and intersegment of hydrocladium, holotype of *Nemertesia octoseriata*, same scale as C. (E) Apophysis, first segment, main- and intersegment of hydrocladium, holotype of *Nemertesia dendritica* (Stechow, 1908), same scale as C.

Nematothecae longer than hydrotheca, conical, movable, adcauline wall of upper chamber depressed. Intersegments long, usually with two median nematothecae (if not lost). Gonothecae arise on apophyses of stems (Fig. 19B), pear-shaped, 0.3–0.35 mm long, opening terminal and perpendicular to long axis, with round operculum.

Dimensions: MHNG-INVE-69620

Distance between hydrocladial whorls: 0.3–0.48 mm

Diameter of stem: 0.16–0.18 mm

Length main segments: 0.19–0.31 mm

Diameter main segment: 0.30–0.40 mm

Length intersegments: 0.21–0.27 mm

Diameter hydrotheca: 60–70 µm

Depth hydrotheca: 40–50 µm

Lateral nematotheca length: 60–70 µm

Type locality: Japan, Kyushu, Hirado Strait, 33°5' - 33°15'N 129°16'–129°15'E, 80 m deep (Jäderholm, 1896).

Distribution: Japan (Sagami Bay to Nagasaki, Okinawa Islands), Korea.

Remarks: The identity and scope of this species and the material from Okinawa was quite difficult to establish. It was necessary to examine the type material of *Nemertesia octoseriata* (Jäderholm, 1896) and *N. dendritica* (Stechow, 1908).

The first Japanese *Nemertesia* species was described by Jäderholm (1896), based on material from near Nagasaki (Hirado Strait, as *Antennularia octoseriata*). Later (1926), Jäderholm synonymised this name with *N. irregularis* (Quelch, 1885), a nominal species based on material from the Cape Verde Islands and nowadays regarded as a synonym of *N. antennina* (Linnaeus, 1758) (Ansín Agís *et al.*, 2001). Jäderholm's material has four hydrocladia per whorl, resulting in eight longitudinal rows of hydrocladia due to the decussate arrangement. The intersegments have one nematotheca only (Fig. 19D). Stechow (1908) then described a new Japanese species *Nemertesia dendritica* with two to three hydrocladia per whorl and two nematothecae per intersegment (Fig. 19E). Shortly afterwards, Stechow (1909) concluded that his *N. dendritica* was identical to *N. perrieri* (Billard, 1901) from the Canary Island, mainly due to the presence of two nematothecae per intersegment. *Nemertesia perrieri* is nowadays regarded as a valid species (Ansín Agís *et al.*, 2001), although some authors think it could be a synonym of *N. antennina*. Molecular results indicate that the situation may be much more complex (Moura *et al.*, 2012).

Hirohito (1995) treated both Jäderholm's and Stechow's species as a synonym of *N. antennina*. Likewise, Park (2010) documented material which is clearly identical to the Okinawa material of this study referring it to *N. antennina*.

During the recent years I have examined dozens of living *N. antennina* colonies from the NE Atlantic and I think

they are distinct from the Japanese ones. However, the only solid diagnostic trait is found in the gonotheca. In Atlantic *N. antennina* and *N. perrieri*, the opening of the gonotheca is always sublateral and inclined sideways (comp. Ansín Agís *et al.*, 2001). In the Japanese material it is terminal and at a right angle to the long axis (Fig. 19B). Other differences are the constant presence of a first ahydrothecate node (Fig. 19B, variable in *N. antennina*), the more delicate stems (about half the diameter), the smaller size, and a more pronounced bundling of the stem bases and a more profuse overgrowth by stolons (well documented by Hirohito, 1995: fig. 89a–b).

Due to these differences – and also the wide separation of the Japanese and European populations – *Nemertesia octoseriata* should therefore be regarded as distinct from *N. antennina* until molecular studies prove the contrary. The molecular studies of Moura *et al.* (2012) on NE Atlantic *Nemertesia* in fact indicate that *N. antennina* is potentially a species complex. This can be used as an argument not to synonymise too readily species with disjunct distributions as it is the case for Japanese and European *Nemertesia*.

Nemertesia octoseriata is paralleling *N. antennina* in its variability and it is not entirely clear if *N. dendritica* is not a distinct species. *Nemertesia dendritica* has 2–3 hydrocladia per whorl, while the type specimen of *N. octoseriata* has four per whorl. Moreover, the former has two nematothecae per intersegment (Fig. 19E), while the latter has one only (Fig. 19D). Both characters usually correlate, meaning colonies with two hydrocladia per whorl have two nematothecae per intersegment (Fig. 19C–B, *dendritica* form), while those with four hydrocladia per whorl have usually one nematotheca per intersegment (*octoseriata* form). Such a correlation of two putatively independent characters is often suggestive for two distinct species being present. However, in the present case it could also be due to environmental factors and more importantly to the age of the stem. Young stems are pinnate and then develop tetraserial hydrocladia. Octoserial stems are likely found in fully grown, old stems only.

Although the material from Okinawa represented the *dendritica* form, some stems had 4–5 hydrocladia per whorl (but still two nematothecae per intersegment). The material from Korea described by Park (2010) appears identical to the Okinawa material. The abundant material examined and described by Hirohito (1995) was evidently very variable and comprised both forms. He depicts the *octoseriata* form (fig. 2), but in one hydrocladium (fig. 2e) there are two nematothecae per intersegment. At present it seems thus reasonable to regard *N. dendritica* as a synonym of *N. octoseriata*, a rather variable species which mirrors the situation in the Atlantic for *N. antennina*, *N. perrieri* and *N. irregularis*.

Nemertesia spec. 1

Fig. 20A-D

Material: MHNG-INVE-91092; Japan, Okinawa Island, Motobu Peninsula, 26.71372°N 127.8786°E, depth 29 m; 19.06.2008; two complete and two partial stems, all sterile.

Diagnosis: Weakly polysiphonic at stem base, 8 cm, a few stems clustered, distal part bearing hydrocladia monosiphonic, hydrocaulus with canaliculate coenosare, regularly segmented, segments short. Each stem segment with two opposite apophyses and about 10 nematothecae, two nematothecae on each apophysis. Apophyses of adjacent segments slightly twisted resulting in hydrocladia being in two times two lateral rows, hydrocladia held laterally and giving impression of stem being pinnate. Hydrocladia up to 12 mm and with up to 16 hydrothecae, segmented homomerously with distinct oblique nodes, segments long, only at ends weakly developed annular thickenings (internal ribs). Hydrotheca elongate cup-shaped, opening at right angle. Three nematothecae per segment, two lateral and one inferior median nematotheca. Nematothecae conical, straight walls, movable, two-chambered, adcauline side somewhat lowered. No gonothecae present.

Dimensions:

Hydrocaulus diameter: 0.5 mm

Hydrocladial segments: 0.6 mm

Hydrotheca depth: 0.3 mm

Hydrotheca diameter: 0.11 mm

Lateral nematotheca: 80 µm

Remarks: Due to the absence of gonothecae, this material was not identified to species level. It strongly resembles *N. cylindrica* (Kirehenpauer, 1876) and *N. indivisa* (Allman, 1883). According to Watson (2000: 51), these two species are hardly distinguishable in the absence of gonothecae. Their gonothecae are quite different, though (for descriptions of *N. cylindrica* see Kirchenpauer, 1876; Watson, 2000; for *N. indivisa* see Allman, 1883; Billard, 1908b, 1913; Schuehert, 2003). The presence of two nematothecae on the stem apophyses favours *N. cylindrica* (4 in *N. indivisa*). The dimensions of the present material slightly surpass the values found in both species: e. g. the segment lengths are 0.6 mm, versus maximally 0.46 and 0.52 mm.

Nemertesia spec. 2

Fig. 21

Material: MHNG-INVE-89123; Japan, Okinawa Islands, SE of Kume Island, 26.2624°N 126.857°E, 150-168 m; 12.11.2009; one stem, without gonothecae.

Diagnosis: Stem 6 cm, unbranched, polysiphonic (including hydrocladia bearing part), thinning out to monosiphonic, main tube with canaliculate coenosare,



Fig. 20. *Nemertesia spec. 1*, MHNG-INVE-91092. (A) Colony silhouettes, note that the stem bases are heavily overgrown by foreign organisms. (B) Part of hydrocaulus (hc) segment with apophysis (ap) followed by begin of hydrocladium. (C) Segment of hydrocladium, note that there are no ahydrothecate segments; same scale as B. (D) Lateral nematotheca seen from adcauline side.

nodes absent. Auxiliary tubes thinner than main tube, with a row of tubercles bearing a pair of nematothecae. Hydrorhiza a tangled mass of thin, stolons anchoring colony in sediment. Hydrocladia held laterally giving impression of stem being pinnate, hydrocladia in two times two rows, 2-3 hydrocladia per whorl. Hydrocladia up to 6 mm and with up to 13 hydrothecae, segmented homomerously with distinct transverse nodes, segments long, with 7-9 conspicuous internal thickenings (ribs). Hydrotheca elongate eup-shaped, opening slightly tilting towards abcauline. Three nematothecae per segment, two lateral and one inferior median nematotheca. Nematothecae long, conical, straight walls, movable, two-chambered, adcauline side somewhat lowered. No gonothecae present.

Dimensions:

Hydrocladial segments: 0.48-0.49 mm

Hydrotheca depth: 0.16-0.21 mm

Hydrotheca diameter: 70-90 μm

Lateral nematotheca: 100-110 μm

Remarks: The present material is likely not fully grown. It is rather distinct from the previous sample and it matches partially the description of *N. japonica* given by Hirohito (1995), except for the depth of the hydrotheca and its opening angle. In the present

material, it is more than two times as deep as in the material of Hirohito from the South China Sea. Additionally, the opening is somewhat inclined towards abcauline instead of being perpendicular to the hydrocladium and the nematothecae appear also longer. Due to the infertile condition and the limited material it was here not identified to the species level.

Genus *Plumularia* Lamarck, 1816

Plumularia habereri Stechow, 1909

Fig. 22

Plumularia habereri Stechow, 1909: 77, pl. 6 fig. 4. – Stechow, 1913: 91, figs 59-60. – Ryland & Gibbons, 1991: 532: fig. 5. – Ansín Agès *et al.*, 2014: 806, figs 9-13.

Plumularia habereri var. *attenuata* Billard, 1913: 42, fig. 34.

Plumularia habereri var. *mucronata* Billard, 1913: 46, fig. 40, pl. 2 fig. 24.

Dentitheca habereri. – Hirohito, 1995: 259, fig. 87a-c.

Not *Plumularia habereri*. – Schuchert, 2003: 211, fig. 60. [= *Plumularia elongata* Billard, 1913]

Not *Dentitheca habereri*. – Di Camillo *et al.*, 2010: 84, figs 2, 3, 5, 6. [= *Plumularia elongata* Billard, 1913]

Material: MHNG-INVE-60992; Japan, Okinawa Island, Mizugama, 26.3590°N 127.7386°E, 9 m; 13.05.2008; almost all nematothecae lost, 11 cm colony, no gonothecae. – MHNG-INVE-60993; Japan, Shikoku Island, Kochi pref., Otsuki, Kochi, 32.7742°N 132.7250°E; 26 m; 26.01.2008; 3.2 cm colony fragment, no gonothecae. – MHNG-INVE-91090; Japan, Okinawa Islands, Okinawa, Cape Hedo, 26.8719°N 128.2657°E, 19.5 m; 21.06.2008, 3 sterile colonies.

Diagnosis: *Plumularia* species forming rather stiff colonies resembling those of Aglaopheniidae, sized

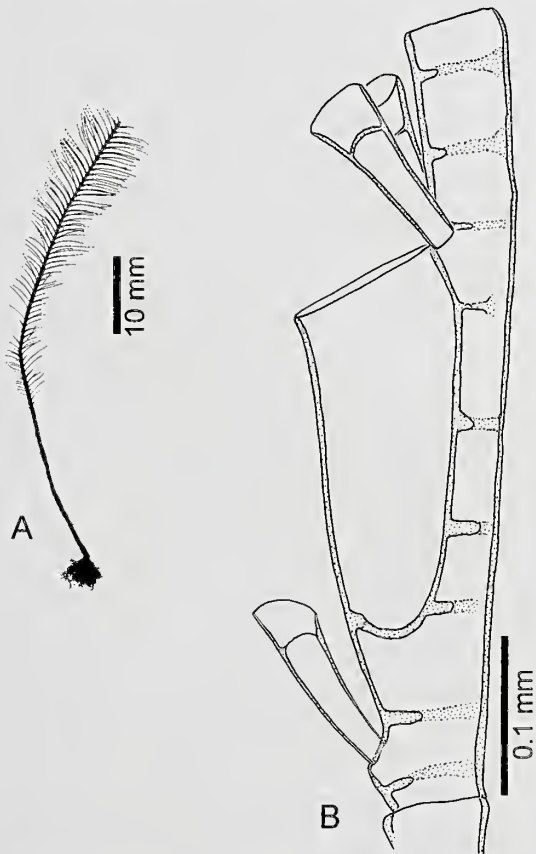


Fig. 21. *Nemertesia* spec. 2, MHNG-INVE-89123. (A) Colony silhouette, distalmost part lost. (B) Hydrocladial segment.

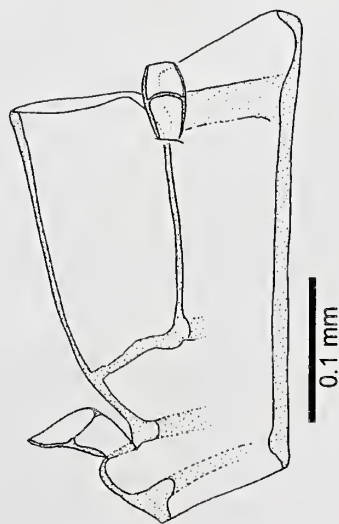


Fig. 22. *Plumularia habereri*, MHNG-INVE-60993; hydrocladial segment.

from a few cm to 28 cm in height, branching in one plane, multipinnate, polysiphonic stem and branches when fully grown. Hydrocladia with homonomous segmentation, short segments, hydrotheca tubular, parallel to segment axis, opening perpendicular to segment axis, deeper than wide, 0.15–0.23 mm deep, adcauline rim deeply lowered. All nematothecae movable and two-chambered. Median inferior nematotheca on bulge of segment. Lateral nematothecae ovoid, reaching above hydrothecal margin. Segment with 3–5 internal ribs, variable. Gonothecae small, on stem apophyses, shaped like inverted cones.

Type locality: Japan, Sagami Bay, Between Ito and Hatsushima Island, depth 150 m (Stechow, 1909).

Distribution: Japan, Philippines, Guam, Indonesia, Chesterfield Island, New Caledonia, and the Coral Sea, depth range 17–460 m (Ansín *et al.*, 2014).

Remarks: The sample 60992 from Okinawa lacks almost all nematothecae. The rather well preserved state of the polyps suggests that the nematothecae have been lost before the colony was collected. Without the nematothecae, this material can be quite difficult to recognize as a *Plumularia* species. A comparison with typical samples from other localities (Fig. 22) showed that it is otherwise identical.

Plumularia habereri has been interpreted as a rather variable species (Schuchert, 2003), although Billard (1913) distinguished and named several varieties, some of which are more likely distinct species (see Ansín Agís *et al.*, 2014). The current material corresponded to the typical form described by Stechow (1909, 1913).

Genus *Sibogella* Billard, 1911

Sibogella erecta Billard, 1911

Fig. 23A–B

Sibogella erecta Billard, 1911: 108. – Billard, 1913: 61, fig. 51, pl. 3 fig. 32. – Hirohito, 1969: 27, fig. 18. – Hirohito, 1995: 282, fig. 97g. – Schuchert, 2003: 217, fig. 64.

Stechowia armata Nutting, 1927: 230, pl. 46 figs 1–2.

Material: MHNG-INVE-69622; Japan, Okinawa Islands, S of Kume Island, 26.24542°N 126.81745°E, 141–165 m; 20.11.2009; colony fragments without gonothecae.

Diagnosis: Plumulariidae with monosiphonic stem, few cm up to 13 cm, main stem with weak nodes, each with a side-branch. Side-branches alternate pinnate or spirally arranged. Side-branches indistinctly segmented, each segment with a sub-terminal apophysis for the attachment of a hydrocladium, stem segments with variable number of nematothecae, 1–2 on main part of segment, 1–3 in upper axil of apophysis, prominent mamelon on apophysis. Hydrocladia modified, flexible,

with heterogeneous segmentation, first segment with or without nematotheca, followed by segment with hydrotheca and the three usual nematothecae, followed by a variable number of up to 2–12 slender segments with 0–2 long nematothecae. Nematothecae all movable, conical, two-chambered, sizes variable. Hydrotheca relatively shallow, wider than deep, adaxial wall adnate to segment, abaxial wall everted, rim smooth. Gonotheca about 0.35 mm, in upper axils of apophyses of side-branches, pyriform.

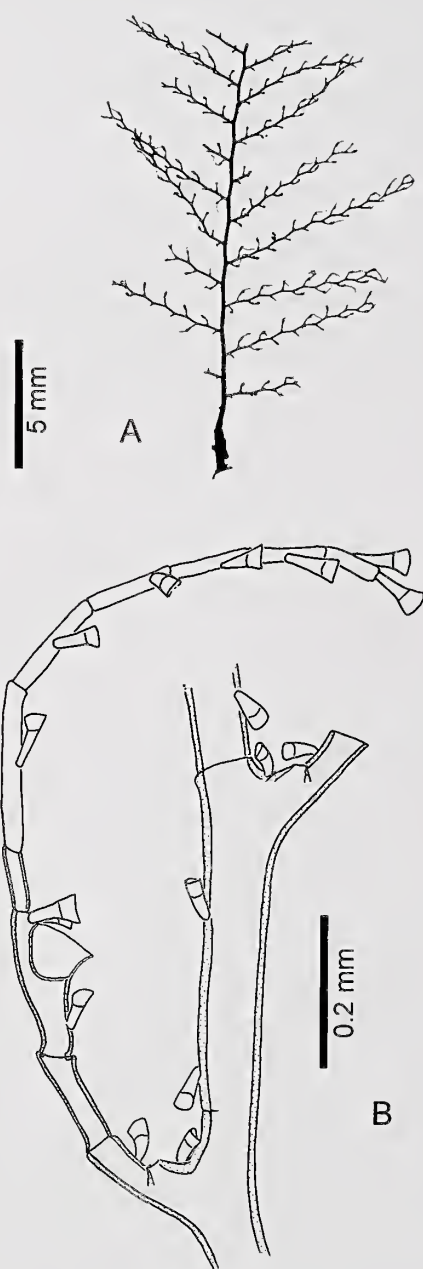


Fig. 23. *Sibogella erecta*, MHNG-INVE-69622. (A) Colony silhouette. (B) Part of side-branch with a modified hydrocladium on left apophysis.

Type locality: Indonesia, between Misool Island and New Guinea, 1.7083°S 130.7917°E, depth 32 m (Billard, 1913).

Distribution: Indonesia, Philippines, Japan (Schuchert, 2003).

Remarks: *Sibogella erecta* with its modified hydrocladia (Fig. 23B) is rather distinct among the Plumulariidae and easily identifiable. The present sample showed some variations when compared to previous description of the species (Billard, 1913; Hirohito, 1995; Schuchert, 2003). The first segment of the hydrocladium (Fig. 23B) always lacked a nematotheca, while it had one in other samples. The segments of the side-branches (Fig. 23B) had usually two nematothecae, while Billard (1913) reported a single one only. Also the apophyses are longer. All these differences are likely only population differences (intraspecific variation).

Family Aglaopheniidae Marktanner-Turneretscher, 1890

Genus Aglaophenia Lamouroux, 1812

***Aglaophenia cupressina* Lamouroux, 1816**

Fig. 24

Aglaophenia cupressina Lamouroux, 1816: 169. – Billard, 1913: 107, fig. 96; pl. 6. – Vervoort, 1941: 233, fig. 11, distribution review. – Millard, 1975: 408, fig. 128A-C. – Schuchert, 2003: 242, fig. 81.

Plumularia bipinnata Lamarck, 1816: 126. – Billard, 1907: 331, synonym.

Aglaophenia macgillivrayi Busk, 1852: 400. – Allman, 1883: 34, pl. 10, pl. 20 figs 4-6. – Billard, 1909: 331, synonym.

Corbulifera macgillivrayi. – Naumov, 1969: 530, figs 380-381.

Material: MHNG-INVE-91091; Japan, Okinawa Island, Cape Hedo, 26.8719°N 128.2657°E, 5 m; 22.06.2008; one fertile colony.

Diagnosis: Large (7-20 cm) colonies, polysiphonic, multipinnate, dense, reminiscent of a fir twig, coenosarc with dense population of zooxanthellae. Hydrotheca relatively small and narrow, narrower than diameter of hydrocladium, depth 0.25-0.30 mm, diameter 0.13-0.15 mm, campanulate, not curved, adcauline side completely adnate. Median inferior nematotheca very stout, breadth in lateral view 2/3 or more of hydrothecal diameter, completely adnate, reaching to the level of hydrothecal rim, with thick, adcauline intrathecal shelf. Hydrocladium with strong internal ribs. Gonothecae in closed corbulae, corbulae 1.7-2.5 mm long.

Description: See Schuchert (2003).

Type locality: Indonesia ("East India", Lamouroux, 1816).

Distribution: Indo-Pacific in warmer waters; from Zanzibar and Mozambique to Great Barrier Reef,

Indonesia, New Guinea, Philippines, Sea of Okhotsk, and Kuriles (Vervoort, 1941; Naumov, 1969; Schuchert, 2003). Occurs even in very shallow water (1 m), but Billard (1913) found it down to 564 m.

Remarks: This species has been reported for Japan as *Corbulifera macgillivrayi* by Naumov (1969), however, it is not clear on what he based this record. Hirohito (1995) did not include *A. cupressina* in his list of Japanese *Aglaophenia* species. The present work is thus likely the first vouchered record of *A. cupressina* for Japanese waters.

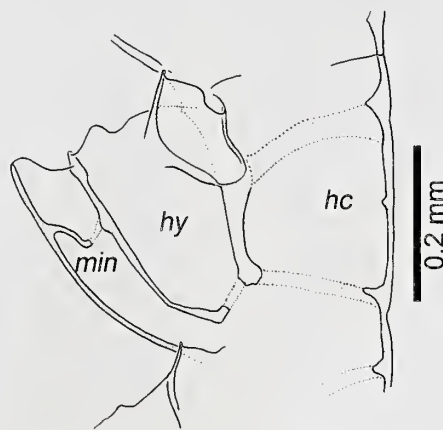


Fig. 24. *Aglaophenia cupressina*, MHNG-INVE-91091. Abbreviations: hc hydrocladium, hy hydrotheca, min median inferior nematotheca

Genus Cladocarpus Allman, 1874

***Cladocarpus bocki* Jäderholm, 1919**

Figs 25A-H, 26A-D

Cladocarpus bocki Jäderholm, 1919: 24, pl. 6 figs 3-4. – Hirohito, 1983: 76, fig. 39. – Hirohito, 1995: 287, fig. 100a-c.

Material: MHNG-INVE-69643; Japan, Okinawa Islands, near Kume Island, 26.3231°N 126.7439°E, 68-99 m; 14.11.2009; one fertile colony (male), hydrorhiza with attached sand. – MHNG-INVE-69662; Japan, Okinawa Islands, near Kume Island, 26.28973°N 126.85767°E, 88-105 m; 10.11.2009; one infertile colony.

Diagnosis: *Cladocarpus* with branched, multi-pinnate colony. In addition to the three standard frontal nematothecae surrounding the hydrotheca, there is an additional single median nematotheca on the rear side of the segment. Hydrotheca long, tubular, rim smooth except for a single abcauline tooth. Long phylactocarps arise basiolateral of hydrothecae, with tubular nematothecae in four rows, with up to 8 gonothecae.

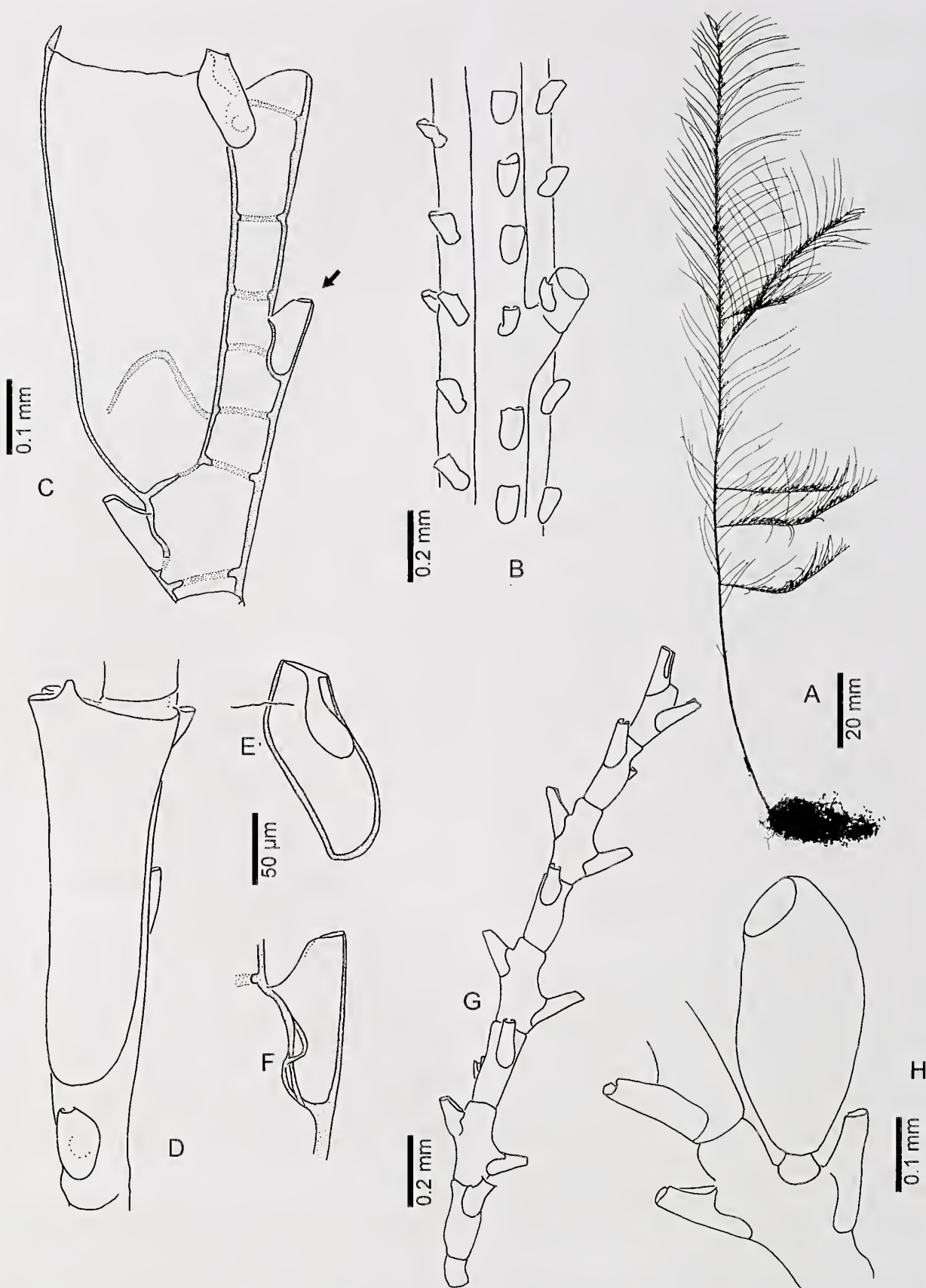


Fig. 25. *Cladocarpus bocki*, MHNG-INVE-69643. (A) Colony silhouette. (B) Polysiphonic branch with one apophysis and rest of broken hydrocladium. (C) Hydrothecate segment, note rear median nematotheca (arrow). (D) Frontal view of Hydrotheca (drawn opaque). (E) Lateral nematotheca seen from adcauline side. (F) Nematotheca on rear side of internode, same scale as E. (G) Phylactocarp without gonothecae. (H) Gonotheca and part of a phylactocarp.



Fig. 26. *Cladocarpus bocki*, MHNG-INVE-69643. (A) Hydrothecate segment, note rear median nematotheca. (B) Polysiphonic branch with one apophysis and rest of broken hydrocladium. (C) male gonotheca. (D) Three phylactocarps bearing gonothecae.

Description: Colony erect, branched, multi-pinnate, hydrocladia alternate, the two rows forming an acute angle (Fig. 25A), stem polysiphonic, arising from a root-like hydrorhiza formed by tubular stolons which anchors the colony in the sediment.

Stem composed of a main tube and numerous auxiliary tubes, thinning out towards distal to monosiphonic condition. Main tube without distinct nodes, with regular apophyses for the hydrocladia and a row of adnate, scoop-shaped nematothecae (Figs 25B & 26B). Auxiliary tubes with one row of adnate nematothecae (Figs 25B & 26B). Hydrocladia long and flexible, homomerously segmented, up to 14-17 segments, each segment (internode) with a deep, campanulate hydrotheca, diameter towards opening slightly increasing, abcauline straight, margin smooth except for a distinct, abcauline tooth. On inside of hydrotheca in lower third a loop-shaped ridge, length variable. Median inferior nematotheca short, reaching just beyond floor of hydrotheca, the pair of lateral nematothecae drop-shaped, upright (Figs 25E). On rear side of segment in median line, a single, adnate, gutter-shaped nematotheca (Figs 25C, 25F, 26A). Each segment with 6-7 distinct internal perisarc ribs.

Gonothecae borne on phylactocarps which arise just lateral to hydrotheca base (Figs 25G, 26D). Phylactocarps develop on the first three segments of the hydrocladium. Phylactocarp composed of up to 8 segments, each with two tubular nematothecae, alternating in positions resulting in four rows of nematothecae. Each segment of the phylactocarp can bear a gonotheca. Gonotheca ellipsoid, opening terminal but oblique (Figs 25I & 26C). Nematocysts: small tentacular capsules (type not identified); large, rounded microbasic heteronemes which can be interpreted as isorhizas or euryteles.

Measurements:

Colony size: up to 200 x 50 mm
 Diameter of main tube: 160 µm
 Distance of hydrocladia of one side: 2.4-2.6 mm
 Length of hydrocladial segments: 640-700 µm
 Hydrotheca opening diameter: 220-230 µm
 Depth of hydrotheca: 520-540 µm
 Height lateral nematotheca: 130-150 µm
 Size median inferior nematotheca: 110-140 µm
 Side rear nematotheca: 100-120 µm
 Length phylactocarp: 2.1-2.3 mm
 Gonotheca: (0.40-0.48)x(0.17-0.20) mm
 Small tentacular capsules: (2)x(5-6) µm
 Large microbasic heteroneme: (6.5-8)x(21-22) µm

Type locality: Okinoshima Island, Kyushu province (Jäderholm, 1919).

Distribution: Okinoshima Island, Sagami Bay (Hirohito, 1983), Nijima Island (Hirohito, 1983), Okinawa Islands (this study).

Biology: On sandy bottoms, known depth range 50-105 m (Hirohito, 1983; this study).

Cladocarpus unilateralis new spec.

Figs 27A-H-28A-E

Holotype: MHNG-INVE-69642, one colony, fertile, 26.2451°N 126.8573°E, Japan, Okinawa Islands, SE Kume Island, 179-192 m, 20.11.2009, triangular dredge.

Diagnosis: *Cladocarpus* with hydrocladia in a single helical row; stem branched, polysiphonic; pair of lateral nematothecae gutter-shaped, very long and clasping hydrothecal margin; a single, lateral supplementary nematotheca in about middle of hydrothecal segment; hydrotheca long, tubular, rim smooth except for a single abcauline tooth. Phylactocarps arising basiolateral of hydrothecae and on opposite side of supplementary nematotheca, with tubular nematothecae in four rows, with a single gonotheca with recurved distal end.

Etymology: The specific epithet refers to the supplementary nematotheca found on one side only.

Description: Colony erect, branched, hydrocladia arranged in a spiral (Fig. 27A), stem polysiphonic, helical, arising from a root-like hydrorhiza formed by tubular stolons. Stem composed of a main tube and numerous auxiliary tubes, thinning out towards distal to monosiphonic condition. Main tube without distinct nodes, with regular apophyses for the hydrocladia and a row of exserted, beaker-shaped nematothecae. Auxiliary tubes with one or more rows of tubular nematothecae sunken into perisarc (Fig. 27B).

Hydrocladia long and flexible, homomerously segmented, 10-15 segments, each segment (internode) with a deep, nearly tubular hydrotheca, diameter towards opening slightly increasing, abcauline wall in side-view undulated, wall in frontal view slightly s-curved, margin smooth except for a distinct, abcauline tooth. In lower third on inside of hydrotheca two loop-shaped ridges. Median inferior nematotheca short, almost completely adnate, reaching just beyond floor of hydrotheca; the two lateral nematothecae elongated, gutter-shaped, clasping hydrotheca along rim leaving only a small median region uncovered (Fig. 27C-D). A single supplementary nematotheca is present on the side of each segment, it is adnate and eup-shaped (Fig. 27C-D). This unilateral supplementary nematotheca is always on the same side of the hydrocladium and also for an entire branch. However the side is different in the two branches of the stem (Fig. 27A). Internodes with 6-7 distinct internal perisarc ribs. Gonothecae borne on phylactocarps which arise just lateral to hydrotheca base (Fig. 27G), always on opposite side of supplementary nematotheca. A single gonotheca per phylactocarp on first segment of phylactocarp. Gonotheca with distal part recurved, often almost 180°, hood-like (Fig. 27G-H). Phylactocarp composed of about four segments, each with two tubular nematothecae, alternating in positions resulting in four rows of tubular nematothecae.

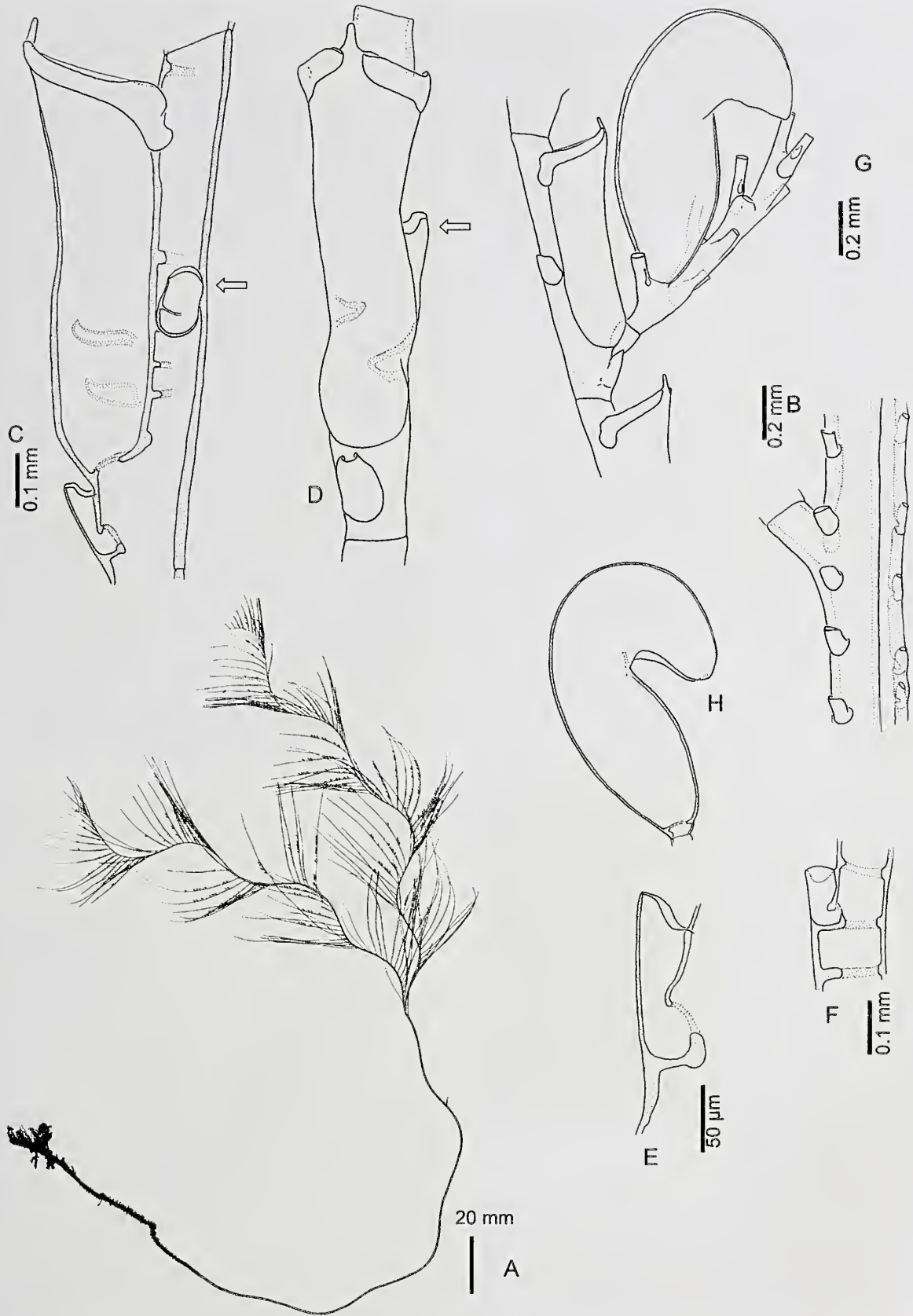
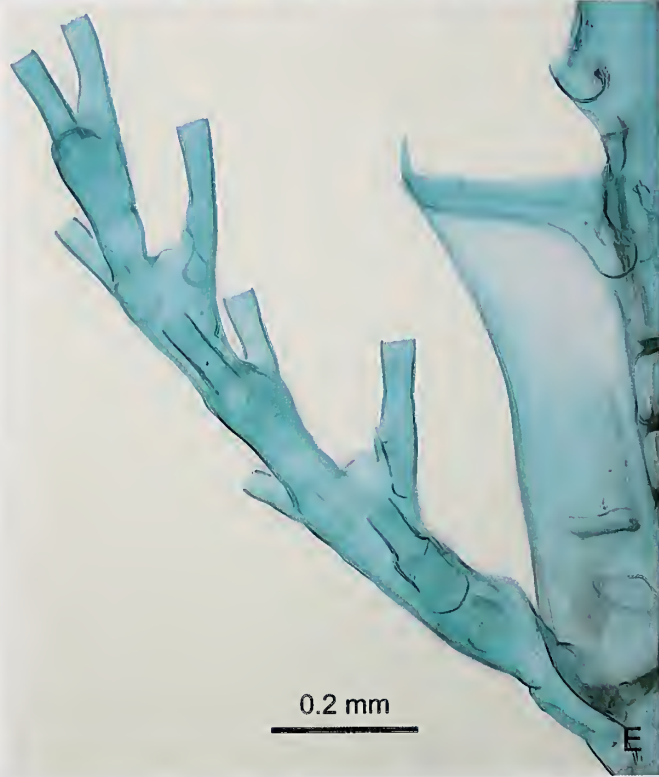
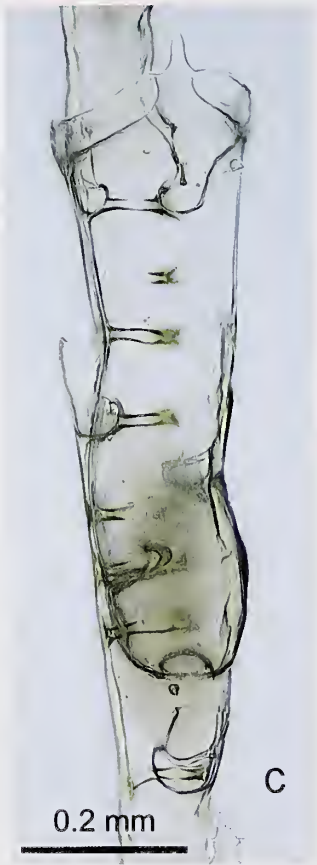
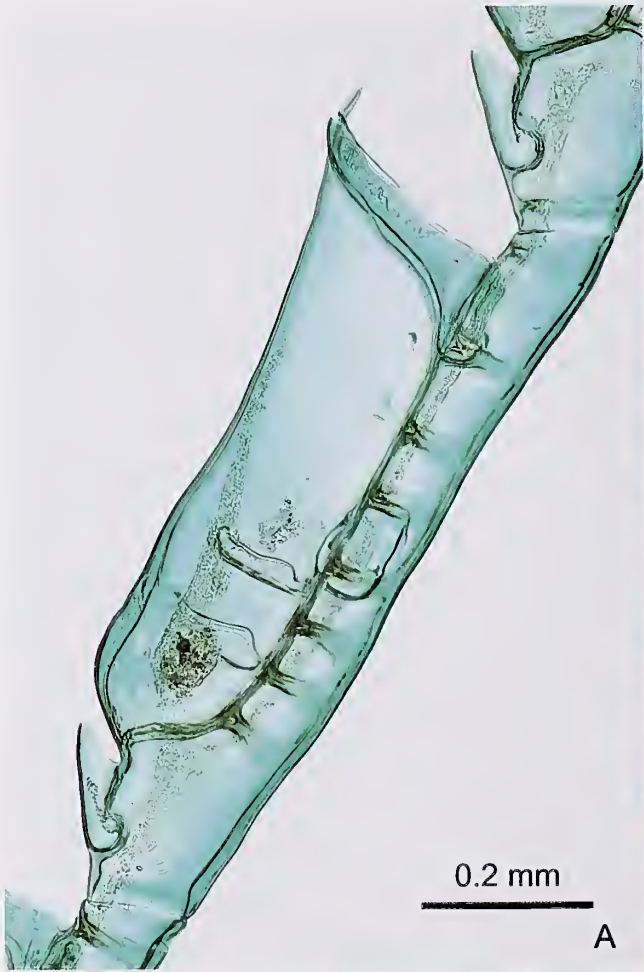


Fig. 27. *Cladocarpus unilateralis* new spec., holotype. (A) Colony silhouette. (B) Part of polysiphonic stem with main tube in front (with apophysis) and an auxiliary tube in rear. (C) Hydrothecate segment in lateral view, note lateral median nematotheca (arrow). (D) Hydrothecate segment in frontal view, note lateral median nematotheca (arrow); same scale as C. (E) Median inferior nematotheca of hydrothecate segment. (F) Unilateral nematotheca of hydrothecate segment seen from rear side. (G) Hydrothecate segment with phylactocarp bearing a gonotheca. (H) Gonotheca in side view; same scale as G.



Measurements:

Colony size: 36 cm high
 Diameter of main tube: 180 μ m
 Distance of hydrocladia: 2.5–3 mm
 Length of hydrocladial segments: 0.85–1.0 mm
 Hydrotheca opening diameter: 0.22–0.24 mm
 Depth of hydrotheca: 0.67–0.74 mm
 Height lateral nematotheca: 70–80 μ m
 Length lateral nematotheca: 280–310 μ m
 Size median inferior nematotheca: 140 μ m
 Side rear nematotheca: 120 μ m
 Length phylactocarp: 2.2 mm
 Gonotheca: 1 mm

Type locality: Japan, Okinawa Islands, SE of Kume Island, 26.2451°N 126.8573°E, 179–192 m.

Distribution: Okinawa Islands.

Remarks: The most conspicuous feature of this species is the spiral arrangement of the hydrocladia (Fig. 27A), contrasting with a strictly pinnate arrangement seen in other congeners (e. g. Fig. 25A, *C. bocki*). This spiral arrangement of the hydrocladia has been deemed diagnostic to separate the genus *Streptocaulus* Allman, 1883 from *Cladocarpus* Allman, 1874 (e. g. Bouillon *et al.*, 2006). The use of this character was rebutted by Ramil & Vervoort (1992b) because the type species of *Streptocaulus* (*S. pulcherrimus* Allman, 1883) has also pinnate growth stages. Ramil & Vervoort (1992b) used the different types of phylactocarps seen in the type species of both *Cladocarpus* and *Streptocaulus* to separate the genera. This was critiqued by Schuchert (2001), as some phylactocarps are intermediate and they are not unambiguously classifiable. A revision of the aglaopheniid genera is highly warranted, but for credible results it is mandatory to base such a revision on a robust molecular phylogeny. A single morphological difference alone is insufficient. Until such a phylogeny based revision is available, I prefer to regard *Streptocaulus* as a synonym of *Cladocarpus*.

At first glance, *Cladocarpus unilateralis* appears somewhat similar to *C. bocki*. But while in the latter species the supplementary hydrotheca is on the rear side of the internode, it is lateral in the present species. Further differences can be found in the form of the paired lateral nematothecae, the number of gonothecae per phylactocarp, the shape of the gonotheca, and also the arrangement of the hydrocladia. The unilateral nematotheca makes *Cladocarpus unilateralis* n. spec. rather unique among its congeners. Other similar species, e. g. *Cladocarpus corneliusi* Ramil & Vervoort, 1992 or *Cladocarpus boucheti* Ramil & Vervoort, 1992, have also supplementary lateral nematothecae, but they are paired

(comp. Ramil & Vervoort, 1992a). These two species also differ in the shape of their upper, lateral nematothecae, as well as the shape of the gonotheca.

The long, lateral nematothecae clasping the hydrotheca are also rather unusual. Similar nematothecae, but with several openings and not with a gutter-shape, can be found in *C. stechowi* Ramil & Vervoort, 1992 and *C. anonymus* Ramil & Vervoort, 1992.

Genus *Gymnangium* Hincks, 1874

Gymnangium expansum (Jäderholm, 1903)

Fig. 29A–B

Halicornaria expansa Jäderholm, 1903: 303, pl. 14 figs 5–7. – Jäderholm, 1919: 26, pl. 6 fig. 7.

Halicornaria sibogae Billard, 1918: 25, fig. 4. – Rees & Vervoort 1987: 165.

Halicetta expansa. – Hirohito, 1995: 293, fig. 103a.

Gymnangium expansum. – Vervoort, 1966: 165, figs 65–66. – Rees & Vervoort, 1987: 163, fig. 3a–b. – Vervoort & Watson, 2003: 289, figs 68G & 69A.

Material examined: MHNG-INVE-69623; Japan, Okinawa Islands, 26.2454°N 126.8174°E, 141–165 m; 20.11.2009; infertile.

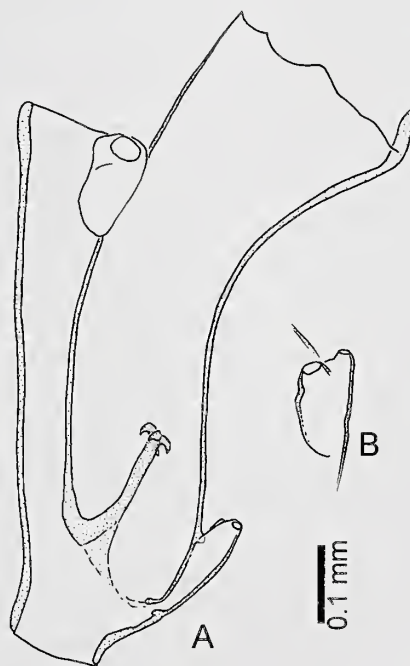


Fig. 29. *Gymnangium expansum*, MHNG-INVE-69623. (A) Hydrothecate segment in lateral view. (B) Median inferior nematotheca in oblique view, note terminal bifurcation; same scale as A.

Fig. 28. Microphotographs of *Cladocarpus unilateralis* new spec., holotype, Fast Blue stained permanent preparations except C. (A) Hydrothecate segment, note unilateral median nematotheca. (B) Phylactocarp with gonotheca. (C) Frontal view of hydrotheca. (D) Lateral view of unilateral nematotheca. (E) Phylactocarp.

Diagnosis: *Gymnangium* species with deep hydrotheca, longer than segment length, 1/3 of adcauline side free, curving away from segment, upper part of hydrotheca expanding, with one sharp, distinct abcauline tooth, 2-3 shallow lateral teeth on hydrothecal rim; adcauline septum often drawn out into a rod ending in a knob with hooks; end of median inferior nematotheca bifid (Fig. 29B).

Description: See Rees & Vervoort (1987).

Type locality: South of Japan, 29.30°N, 125.67°E, 104 m (Rees & Vervoort, 1987).

Distribution: Japan, New Zealand, Indonesia, eastern Africa (Rees & Vervoort, 1987; Vervoort & Watson, 2003).

Remarks: This is a characteristic species that can reliably be identified even in the absence of gonothecae (Fig. 29A-B).

Gymnangium roretzii
(Marktanner-Turneretscher, 1890)

Fig. 30A-K

Aglaophenia roretzii Marktanner-Turneretscher, 1890: 271, pl. 6 figs 22 & 22a.

Gymnangium roretzii. – Stechow, 1909: 102, pl. 6 fig. 18. – Hirohito, 1995: 290, fig. 101f.

Material examined: Part of holotype colony, NMW, registration number 6015, alcohol preparation, origin Japan, collected by Roretz, identified by Marktanner-Turneretscher, without further collection data. – MHNG-INVE-69634; Japan, Okinawa Islands, N of Kume Island, 26.3932°N 126.7535°E, 95.5-123 m; 19.11.2009; infertile. – MHNG-INVE-69645; Japan, Okinawa Islands, S of Kume Island, 26.2545°N 126.7946°E, 114-115 m; 13.11.2009; infertile.

Diagnosis: Similar to *G. allmani* (Marktanner-Turneretscher, 1890) and *G. hians* (Busk, 1852), but rim of hydrotheca with one pair of lateral cusps only, the cusps variable, often drawn out and recurved like a wing.

Description (Okinawa material): Colonies forming pinnate stems, monosiphonic, thick, mostly without distinct nodes. Hydrorhiza composed of few tubular stolons. Hydrocladia stiff, dense, regularly spaced (Fig. 30A), similar in length, alternate in position, both series in about the same plane, this plane tangential to stem and thus defining an anterior and posterior side of the plume.

Stem nematothecae associated with apophyses of hydrocladia in groups of three, two anterior and one axillar on rear side of plume; lower anterior sacciform, one elongated opening (Fig. 30E), upper anterior nematotheca saceiform with two openings, one elongate, the other on a conical protrusion (Fig. 30E); rear nematotheca on

upper axil sac-like, two openings, one opening elongate, the other on a very long, tubular appendage (Fig. 30F). Hydrocladia homomerously segmented (Fig. 30B-D), nodes indistinct, branch thick, hydrotheca almost as large as segment; hydrotheca cup-shaped, almost perpendicular to segment axis, relatively long free adcauline part, in about middle of abcauline wall a horizontal septum which spans at least 2/3 of diameter, septum somewhat concave, free rim of septum swollen and usually with teeth (Fig. 30B-C); rim of hydrotheca with one broad lateral cusp on each side, these variable but usually long and recurring and resembling two wings in frontal view (Fig. 30C-D); abcauline wall of hydrotheca often with a kink (Fig. 30B, D). The three usual nematothecae associated with the hydrotheca; the pair of lateral nematothecae sac-shaped to triangular, large adcauline opening (Fig. 30C); median inferior nematotheca very long (Fig. 30B-D), tubular, curved, spanning about 2/3 of hydrothecal opening, adnate along whole abcauline side of hydrotheca, with a terminal opening and an elongated opening on upper side where becoming free from hydrotheca.

Gonothecae absent in present material, see Hirohito (1995) for an illustration.

Measurements: Sample MHNG-INVE-69645 and holotype

Colony size: 12 cm

Diameter of main tube: 0.31-0.5 mm

Distance of hydrocladia of one side: 0.75-1.05 mm

Length of hydrocladial segments: 0.33-0.41 mm

Hydrotheca opening diameter: 0.18-0.29 mm

Depth of hydrotheca: 0.23-0.28 mm

Height lateral nematotheca: 80-150 µm

Size median inferior nematotheca: 125-230 µm

Type locality: Japan (Marktanner-Turneretscher, 1890).

Distribution: Japan.

Remarks: The new material from the Okinawa Islands was only hesitatingly attributed to *G. roretzii* as both available colonies lacked gonothecae. *Gymnangium roretzii*, a species only known from Japan, is somewhat difficult to separate from the Indo-Pacific *G. hians* (see Watson, 2000, description of material from close to type locality) as well as the Atlantic *G. allmani* (Marktanner-Turneretscher, 1890) (see Galea, 2013 for a recent description). While these two species have typically a hydrothecal rim with two pairs of teeth, *G. roretzii* has only one. It may be, however, rather variably developed (see Fig. 30G-I). Indo-Pacific *G. allmani* have also been described as having one pair of hydrothecal cusps only (Billard, 1913; Jäderholm, 1923; Millard, 1975). Galea (2013) regarded these Indo-Pacific *G. allmani* as distinct from the true *G. allmani* which is an Atlantic species. Perhaps some Pacific records of *G. allmani* could in fact belong to *G. roretzii*. Other, small differences can be found in the nematothecae of the stem, in particular

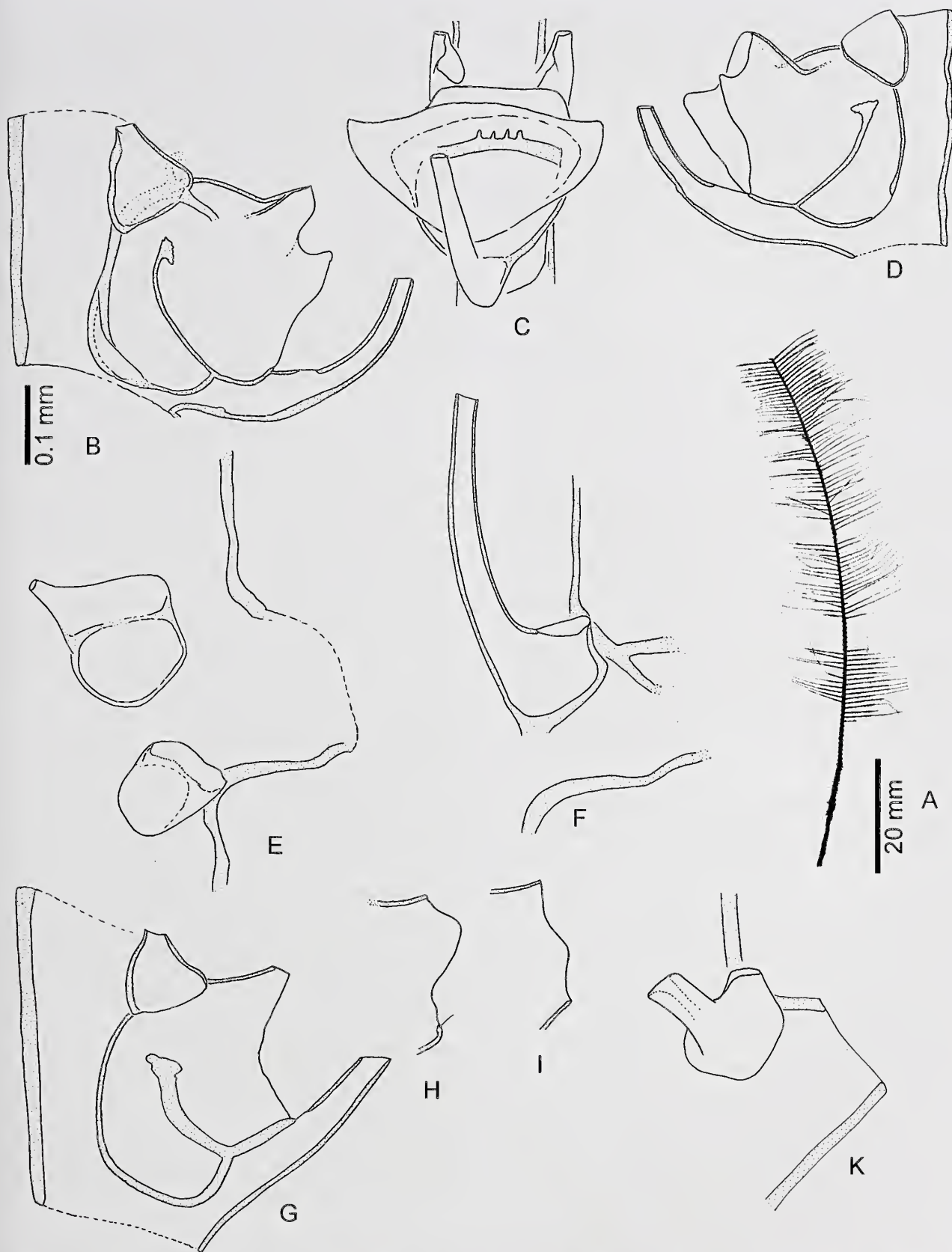


Fig. 30. *Gymnangium roretzii*, material from the Okinawa Islands, except G-K which is type material. Scale bar in B is valid for B through K. (A) Colony silhouette. (B) Lateral view of hydrothecate segment. (C) Frontal view of hydrothecate segment. (D) Oblique view of hydrothecate segment. (E) Apophysis of stem, frontal side, note two nematothecae. (F) Apophysis of stem, rear-side, note nematotheca with very long tubular process. (G) Lateral view of hydrothecate segment of holotype. (H-I) Variation of lateral cusps of hydrothecal rim, holotype. (K) Apophysis of stem, rear-side, note nematotheca with moderately long tubular process, holotype.

the one on the rear-side of the apophyses bearing the branches. While *G. allmani* has a flat, sac-like shape with several openings on short processes (Galea, 2013), it is simple like a lateral nematotheca in *G. hians* (see Watson, 2000). In *G. roretzii* it is also sac-like, but has two distinct openings: one elongate slit-like and one at the end of a tubular extension (Fig. 30F, K). In the new material, this axillar nematotheca differed significantly from the type material in that the tubular extension is very long and conspicuous (Fig. 30F). It is therefore possible that the present material could belong to a separate, unnamed species.

Genus *Lytocarpia* Kirchenpauer, 1872

Lytocarpia delicatula (Busk, 1852)

Fig. 31

Plumularia delicatula Busk, 1852: 396.

Aglaophenia delicatula. – Bale, 1884: 167, pl. 14 fig. 4, pl. 17 fig. 11. – Billard, 1913: 106, fig. 95. – Jäderholm, 1920: 8, pl. 2 fig. 7. – Watson, 2000: 57, fig. 46A-E.

Thecocarpus delicatulus. – Millard, 1975: 455, 139D-E.

Lytocarpia delicatula. – Schuchert, 2003: 235, fig. 76. – Di Camillo *et al.*, 2011: 527, figs 2d; 3c, f; 6e; 9a-g; 10a-i.

Material examined: MHNG-INVE-69635; Japan, Okinawa Islands, 26.3605°N 126.6876°E, 86-97 m; 19.11.2009; with developing corbulae. – MHNG-INVE-69656; Japan, Okinawa Islands, 26.3474°N 126.6886°E, 96-186 m; 19.11.2009; with developing corbulae.

Diagnosis: *Lytocarpia* species with monosiphonic, unbranched stem, usually 3-5 cm. Hydrotheca

campanulate, depth 0.21-0.23 mm; one sharp, long, thick abcauline tooth, rim with two broad lateral cusps on each side; with short adcauline shelf continued as ridge to abcauline wall. Median inferior nematotheca reaching same level as rim of hydrotheca. Corbula open, costae thin, not flattened, widely separated.

Description: Schuchert (2003), Di Camillo *et al.* (2011).

Type locality: Australia, Queensland, Torres Strait, Prince of Wales Channel, depth 16 m (Busk, 1852).

Distribution: Northern Australia, Great Barrier Reef, Australia, Indonesia, Seychelles, Maldives Islands, Moçambique (Di Camillo *et al.*, 2011). New record for Okinawa Islands (this study).

Lytocarpia nigra (Nutting, 1906)

Fig. 32A-B

Thecocarpus niger Nutting, 1906: 953, pl. 5 fig. 5, pl. 13 figs 1-6. – Stechow, 1913: 96, figs 65-67.

Lytocarpia niger. – Rho, 1967: 346, fig. 7A-B, pl. 1 fig. 1.

Lytocarpia nigra. – Hirohito, 1995: 295, fig. 104c-e.

Material examined: MHNG-INVE-69663; Japan, Okinawa Islands, 26.3283°N 126.7160°E, 93-101 m; 19.11.2009; infertile. – MHNG-INVE-69630; Japan, Okinawa Islands, 26.3932°N 126.7535°E, 95.5-123 m; 19.11.2009; infertile.

Diagnosis: Similar to *L. delicatula*, but entire coenosarc of colony with black pigment, colony up to 20 cm, branched (multipinnate), stem polysiphonic. Hydrotheca deeply campanulate, depth about 0.33 mm, in lower half a horizontal ridge along inside of wall; cusps very tall, 9 in total, one curved median abcauline tooth, on each side four lateral cusps of which the three anterior ones are rounded and the fourth is pointed, the embayments between the median and the rounded cusps strongly everted and giving the rim of the hydrotheca a folded appearance (Fig. 32B). Corbula open, costae thin, not flattened.

Description: See Nutting (1906) or Stechow (1913).

Type locality: USA, Hawaii, Laysan Island (Nutting, 1906).

Distribution: Hawaii (Nutting, 1906), Sagami Bay (Stechow, 1913; Hirohito, 1995), Okinawa Islands (this study), Korea (Rho, 1967).

Lytocarpia orientalis (Billard, 1908)

Fig. 33

Thecocarpus myriophyllum var. *orientalis* Billard, 1908a: 73, fig. 1. – Billard, 1913: 91, fig. 76-78, pl. 5 fig. 43. – Jäderholm, 1919: 25, pl. 6 fig. 5.

Thecocarpus myriophyllum var. *elongatus* Billard, 1910: 51.

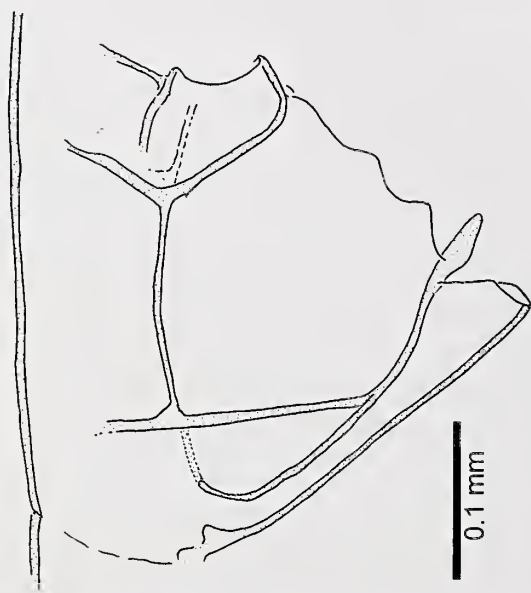


Fig. 31. *Lytocarpia delicatula* MHNG-INVE-69635, lateral view of hydrotheca.

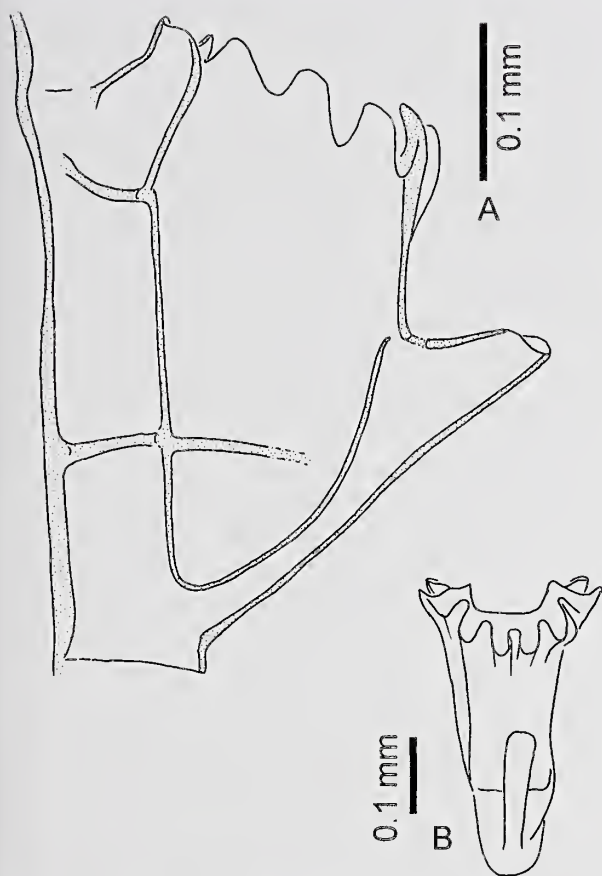


Fig. 32. *Lytocarpia nigra* MHNG-INVE-69663. (A) Lateral view of hydrotheca. (B) Frontal view of hydrotheca, note pleated rim.

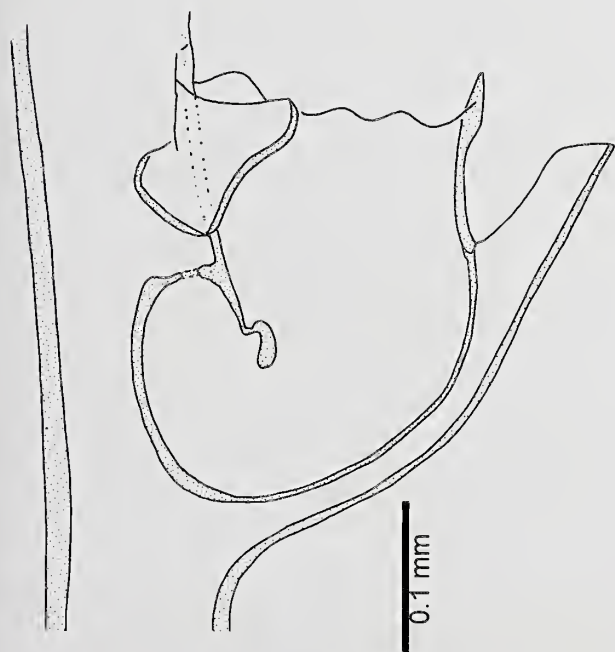


Fig. 33. *Lytocarpia orientalis* MHNG-INVE-69644, lateral view of hydrotheca.

Thecocarpus myriophyllum var. *angulatus* Billard, 1913: 94, figs 79-80.

Gymnangium unjinense Watson, 2000: 62, fig. 50A-E.

Lytocarpia orientalis. – Schuchert, 2003: 240, fig. 79.

Material examined: MHNG-INVE-87092; Japan, Okinawa Islands, 26.2454°N 126.8174°E, 141-165 m; 20.11.2009; infertile. – MHNG-INVE-88803; Japan, Okinawa Islands, 26.2776°N 126.8914°E, 151-160 m; 12.11.2009; with corbulae. – MHNG-INVE-69644; Japan, Okinawa Islands, 26.2838°N 126.8659°E, 126-136 m; 12.11.2009; with corbulae.

Diagnosis: *Lytocarpia* species resembling *L. myriophyllum* (Linnaeus, 1758), but stems never branched, median inferior nematotheca attached along 2/3 of abcauline wall of hydrotheca, free end reaching almost to rim level of hydrotheca. Costae of corbula fused to form a tube, costae broad, flattened.

Description: See Schuchert (2003).

Type locality: Not designated, Billard's (1908a) two samples came from Indonesia, Borneo, 3.45°S 117.60°E 59 m depth, and north of the island Waigeo, 0.220°N 130.401°E 141 m depth (data from Billard, 1913).

Distribution: Japan, Indonesia, Philippines, northern Australia, Chile (Schuchert, 2003).

Remarks: The material matched very well the specimens described in Schuchert (2003). The species has already been recorded in Japanese waters by Jäderholm (1919).

Genus *Macrorhynchia* Kirchenpauer, 1872

Macrorhynchia balei (Nutting, 1906)

Fig. 34

Lytocarpus balei Nutting, 1906: 954, pl. 6: fig. 1, pl. 13: figs 7-8. – in part Stechow, 1909: 99, pl. 6: figs 12-13. – Billard, 1913: 81, fig. 66. – Nutting, 1927: 236. – Vervoort, 1941: 226, fig. 9.

not *Lytocarpus balei*. – Leloup, 1930: 8, fig. 6, pl. 1: fig. 3. – Hirohito, 1995: 297, fig. 105a-c. [= *M. philippina*]

? *Macrorhynchia philippina*. – Hirohito, 1983: 78, fig. 41. – Hirohito, 1995: 297, fig. 105d-g. [not *Macrorhynchia philippina* Kirchenpauer, 1872]

Macrorhynchia balei. – Schuchert, 2003: 226, fig. 71.

Material examined: MHNG-INVE-69640; Japan, Okinawa Islands, SE of Kume Island, 26.2836°N 126.9007°E, 142-149m; 13.11.2009; with gonothecae. – MHNG-INVE-89124; Japan, Okinawa Islands, SE of Kume Island, 26.2624°N 126.857°E, 150-168 m; 12.11.2009; sterile.

Diagnosis: *Macrorhynchia* species with pores in hydrocladial wall opposite of hydrotheca, these pores associated with bundles of long nematocysts (Fig. 34), more distal segments of the hydrocladium may lack the pore).

Description: See Schuchert (2003).

Type locality: Off south coast of Molokai, Hawaiian archipelago, 86–210 m (Nutting, 1906).

Distribution: Hawaii (Nutting, 1906), Indonesia (Schuchert, 2003), Philippines (Nutting, 1927), Japan (Stechow, 1909; this study).

Remarks: The present samples was not separable from Indonesian material described by myself in 2003. The phylactocarps had two to eight gonothecae. The auxiliary tubes of the stems had rows of holes for nematophores.



Fig. 34. *Macrorhynchia balei*, MHNG-INVE-69640, lateral view of hydrothecate segment, note the pore on the rear side (arrow) which serves as opening to discharge the large nematocysts which occur in clusters close to the opening (only a few capsules shown).

***Macrorhynchia fulva* Di Camillo, Puce & Bavestrello, 2009**

Fig. 35A–E

Macrorhynchia fulva Di Camillo *et al.*, 2009: 13, figs 2C–E, 4A–G.

Material examined: MHNG-INVE-87091; Japan, Okinawa Islands, S of Kume Island, 26.2454°N 126.8174°E, 141–165 m; 20.11.2009; infertile. –

MHNG-INVE-69649; Japan, Okinawa Islands, SE of Kume Island, 26.2624°N 126.8570°E, 50–168 m; 12.11.2009; infertile.

Diagnosis: Like *Macrorhynchia phoenicea*, but with a distinct, tongue-like projection on adcauline side of hydrothecal rim (Fig. 35A, arrow) and lateral nematothecae whose openings are directed sideways in proximal segments (Fig. 35C).

Description: Colonies fan-shaped, regularly multi-pinnate, reaching heights of 10 cm and more, attached to a root-like hydrorhiza composed of tubular stolons. Stem and major side branches polysiphonic in basal part, thinning out to monosiphonic in distal part, in polysiphonic parts composed of a superficial primary tube bearing hydrocladia and several auxiliary tubes. Stem light brown to dark brown in older parts or colonies. Auxiliary tubes without nematothecae. Proximal portions of the primary tubes in stem and branches bearing frontal nematothecae only and no hydrocladia, these nematothecae like those in hydrocladia-bearing parts. Primary tube of stem with somewhat indistinct segmentation (nodes), each internode with a hydrocladium, hydrocladia alternating sides, associated with hydrocladium on frontal side of primary tubule are two nematothecae, sac-like with an oval distal opening and a conical, nematotheca-like process with a terminal opening (Fig. 35E). Near base of hydrocladium a mamelon (short, conical process with distal opening). Hydrocladia segmented by transverse nodes, up to 13 segments per hydrocladium, hydrocladia alternate, more or less parallel.

Hydrotheca large, bowl-shaped, no or almost no free ab- and adcauline sides, one large, thick intrathecal septum on abcauline side, its end thickened with irregular prickles. Inside hydrotheca, on upper adcauline wall a shallow, keel-like vertical septum which is continued externally as a characteristic, tongue-like process (Fig. 35A–D). Hydrothecal rim with one broad lateral tooth which is flaring. Behind hydrotheca three thick annular ridges.

Median inferior nematotheca tubular, tapering, overtopping hydrothecal opening but length variable, one terminal opening and one oval opening on adcauline side where fused to hydrotheca. Lateral nematothecae, small, volcano-shaped, terminal opening directed sideways in proximal segments (Fig. 35C), in the distal-most segments opening directed along the hydrocladial axis (Fig. 35D). Lateral nematothecae have a second, adcauline opening near base.

Reproductive structures not observed, for a description see Di Camillo *et al.* (2009).

Measurements: (in brackets values of type material according to Di Camillo *et al.*, 2009)

Colony size: height 5–10 cm (2.5 cm)

Diameter of main tube: 140–160 μ m

Distance of hydrocladia: 0.55–0.58 mm (0.3–0.35 mm)

Length of hydrocladial segments: 0.26-0.27 mm (0.275-0.285 mm)

Hydrotheca opening diameter: 140-150 μ m (185-190 μ m)

Lateral nematotheca: 45-50 μ m (80-145 μ m)

Type locality: Indonesia, North Sulawesi, Bunaken National Marine Park, Mandolin, depth 18 m (Di Camillo *et al.*, 2009).

Distribution: Indonesia (Di Camillo *et al.*, 2009), Okinawa Islands (this study).

Remarks: The present material was assigned to

M. fulva due to the characteristic, tongue-like process of solid perisarc found at the adcauline rim of the hydrotheca (Fig. 35A-B). Some differences to the Indonesian material described by Di Camillo *et al.* (2009) were nevertheless observed. The lateral cusps of the hydrotheca are somewhat smaller and less flaring. More importantly, there are some obvious size differences (see Measurements above). These differences were interpreted as intraspecific variation.

Di Camillo *et al.* (2009) give as a further diagnostic character of this species the “sideways directed lateral nematothecae”. In the here examined material they are not always directed sideways. In the more distal

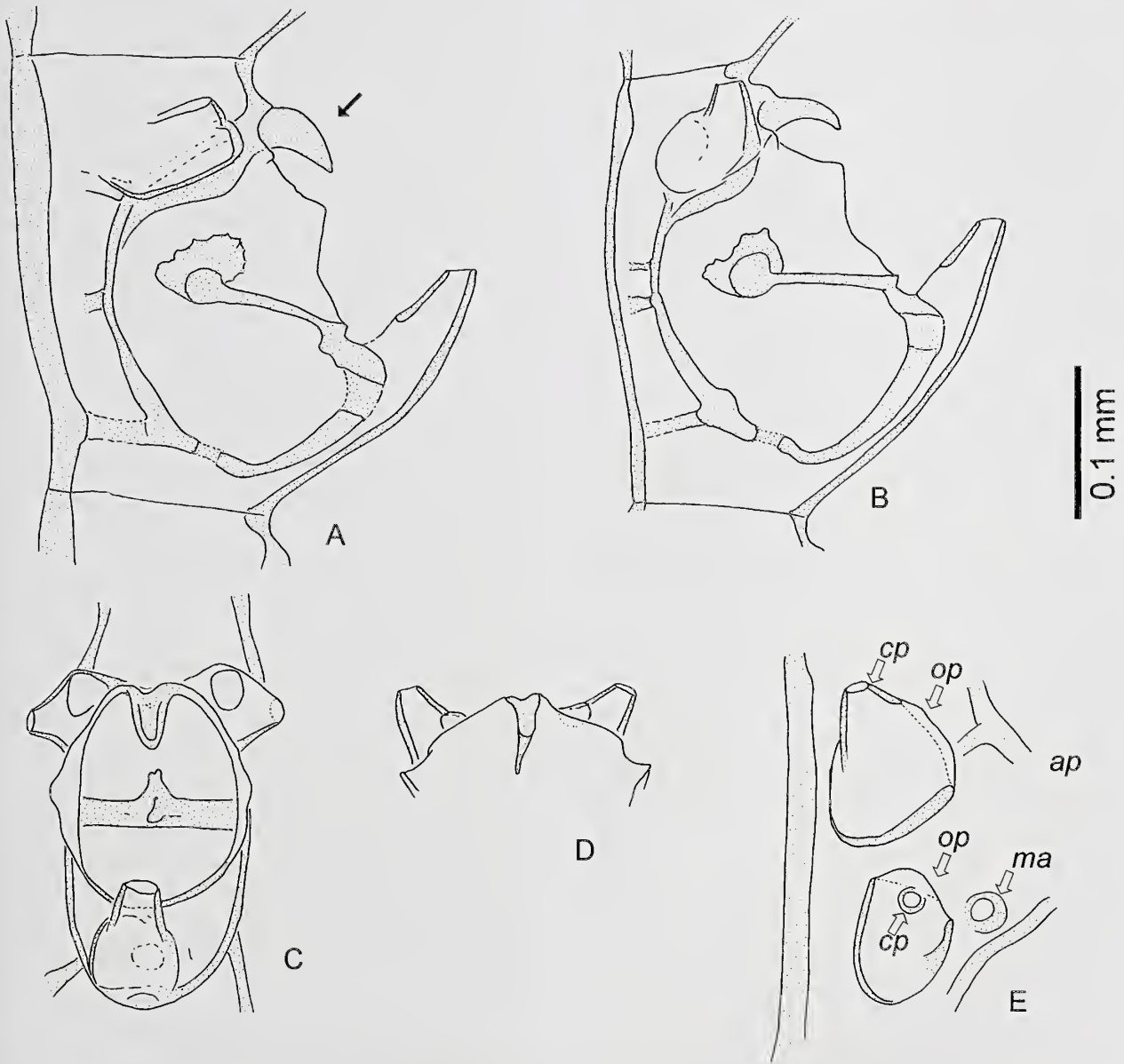


Fig. 35. *Macrorhynchia fulva*, all MHNG-INVE-69649, except B which is MHNG-INVE-87091. (A) Lateral view of hydrotheca of a proximal segment of the hydrocladium. (B) Lateral view of hydrotheca of a distal segment. Besides the shape of the lateral nematothecae, there is not much variation. (C) Hydrotheca in frontal view, proximal segment; the lateral nematothecae point sideways. (D) Hydrothecal opening in frontal view and lateral nematothecae of a distal segment; the lateral nematothecae point more upwards. (E) Main tube of stem with base of apophysis (*ap*) and two nematothecae resembling modified hydrothecae; *cp* = conical protrusion with terminal opening, *op* = opening of theca, *ma* = mamelon. The scale bar applies to all figures.

segments of the hydrocladium they are more or less upright (Fig. 35D). However, even in the type material this seems to be ease (comp. fig. 4D in Di Camillo *et al.*, 2009).

***Macrorhynchia crestata* new spec.**

Figs 36A-I, 37

Holotype: MHNG-INVE-69639; Japan, Okinawa Islands, SE of Kume Island, 26.2836°N 126.9007°E, 142-149 m; 13.11.2009, fertile colony.

Paratypes: MHNG-INVE-88807; Japan, Okinawa Islands, SE of Kume Island, 26.2836°N 126.9007°E, 142-149 m; 13.11.2009, fertile colonies, same batch as holotype colony. – MHNG-INVE-69621; Japan, Okinawa Islands, S of Kume Island, 26.2545°N 126.7946°E, 114-115 m; 13.11.2009; fertile colony. – MHNG-INVE-87096; Japan, Okinawa Islands, S of Kume Island, 26.2454°N 126.8175°E, 141-165 m; 20.11.2009; infertile colony. – MHNG-INVE-87097; Japan, Okinawa Islands, SE of Kume Island, 26.2962°N 126.8968°E, 90-91 m; 13.11.2009; infertile colony. – MHNG-INVE-87240; Japan, Okinawa Islands, S of Kume Island, 26.2579°N 126.7871°E, 116-125 m; 20.11.2009; infertile colony.

Diagnosis: Like *M. phoenicea*, but with an adcauline, vertical keel-like intrathecal septum which is larger than in *M. fulva* and not protruding out of the hydrotheca as a tongue-like process. Nematothecae lateral of hydrotheca with opening directed upwards.

Etymology: The specific epithet “*crestata*” refers to the vertical, keel-like intrathecal septum.

Description: Colonies delicate, fan-shaped, multi-pinnate (Fig. 36A), reaching height of 11 cm and width of 5 cm, attached via a root-like hydrorhiza composed of tubular stolons. Stem and major side branches polysiphonic in basal part and thinning out to monosiphonic in distal part, in polysiphonic parts composed of a superficial primary tube bearing hydrocladia and several auxiliary tubes. Auxiliary tubes without nematothecae. Primary tube of side branches originating from auxiliary tubes. Proximal portions of the primary tubes in stem and branches bearing frontal nematothecae only and no hydrocladia, these nematothecae like those in hydrocladia-bearing parts. Primary tube of stem with distinct to indistinct segmentation (nodes), each internode with a hydrocladium on alternate sides. Associated with each hydrocladium on frontal side of primary tubule are two nematothecae, sac-like, with an oval distal opening and a conical nematotheca-like process with a terminal opening (Fig. 36B-C). Near base of hydrocladium a mamelon (short, conical process with distal opening). Hydrocladia alternate, more or less parallel, segmented

by transverse or slightly oblique nodes, up to 10 segments per hydrocladium. Hydrotheca large, bowl-shaped, short free adcauline side, very short or no free abcauline side, one large, thick intrathecal septum on abcauline side, its end curled and thickened with irregular prickles, small adcauline septum above pore for polyp. Near rim of adcauline side a distinct and characteristic keel-like vertical septum (Figs 36D-F, 37). Hydrothecal rim with one broad and a smaller, more adcauline tooth (Fig. 36F), position, size, and shape of teeth rather variable (Fig. 36H). Behind hydrotheca three thick annular ridges. Median inferior nematotheca tubular, tapering, overtopping hydrothecal opening but length variable, one terminal opening and one oval opening on adcauline side where fused to hydrotheca. Lateral nematothecae conical, shape variable, terminal opening directed along axis of hydrocladium, second opening adcauline near base. Gonothecae on modified hydrocladia (phylactocarps) replacing a normal hydrocladium. One gonotheca per phylactocarp, lentil-shaped, in proximal part two wings flanking attachment stalk (Fig. 36I). First segment of phylactocarp a normal hydrothecate segment, followed by an unsegmented tube with initially two rows of long, conical nematothecae, more distally three indistinct rows of nematothecae. Gonotheca attached distal to hydrothecate segment.

Measurements (all type material):

Colony size: height 5-11 cm, width 5 cm

Diameter of main tube: 115-145 µm

Distance of hydrocladia of one side: 0.49-0.81 mm

Length of hydrocladial segments: 0.29-0.35 mm

Hydrotheca opening diameter: 130-180 µm

Height lateral nematotheca: 30-70 µm

Size median inferior nematotheca: 85-170 µm

Length phylactocarp: 1.7 mm

Gonotheca: 0.25 mm

Large microbasic heteroneme: ca 70 µm long

Type locality: Japan, Okinawa Islands, SE of Kume Island, 26.2836°N 126.9007°E, 142-149 m.

Distribution: Okinawa Archipelago, Kume Island.

Remarks: *Macrorhynchia crestata* resembles closely *M. fulva*, particularly in the macroscopic aspect of the colony and the microscopic morphology of the hydrotheca (comp. Figs 35A-B and 36D-E).

Macrorhynchia crestata can be distinguished from *M. fulva* by:

- the clear absence of the tongue-like process protruding on the adcauline side of the hydrothecal rim,
- the larger intrathecal, vertical keel,
- the lateral nematothecae which are always directed along the axis of the segment (Fig. 36G).

The currently known material of both nominal species seems distinct, but it is possible that both nominal species are only variants that become inseparable once more specimens and a more complete knowledge of the

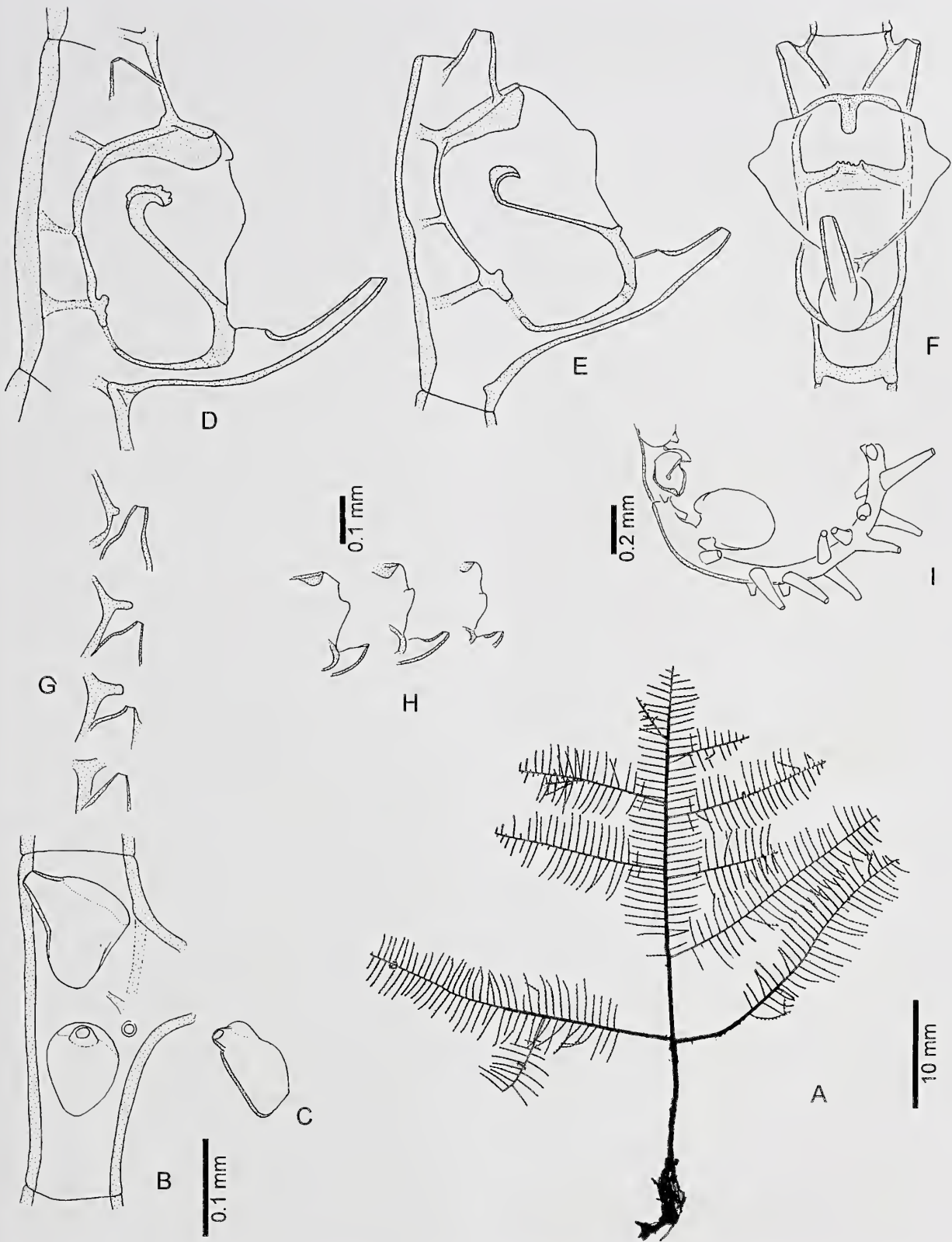


Fig. 36. *Macrorhynchia crestata* n. spec. all MHNG-INVE-69639 (holotype), except H which is from MHNG-INVE-87097. If not otherwise indicated, all magnifications are as in B. (A) Colony silhouette. (B) Segment of main tube of stem, apophysis of cladium directed towards right. Two nematothecae with conical processes are present. The double circle at the base of the apophysis is a mamelon (compare also Fig. 35E). (C) Lateral view of lower nematotheca depicted in B. (D) Lateral view of hydrothecate segment in proximal region of cladium. (E) Lateral view of hydrothecate segment in distal region of cladium. (F) Frontal view of hydrothecate segment. (G) Variation of the lateral nematotheca from proximal (below) to distal (top). (H) Variation of hydrothecal rim within the same colony. (I) Phylactocarp with a single gonotheca.

variation are known. A molecular genetic study is in progress and will hopefully provide additional arguments. In order to facilitate discussion, it is preferable to have a name for this form.



Fig. 37. *Macrorhynchia crestata* n. spec. MHNG-INVE-69639 (holotype), photograph of lateral view of hydrotheca (focus stacking image).

ACKNOWLEDGEMENTS

My sincere thanks go to Frédéric Sinniger for providing the samples of this study. Thanks are also due to Paulyn Cartwright (University of Kansas) who determined the two 16S sequences.

REFERENCES

Agassiz L. 1862. Contributions to the natural history of the United States of America. Vol. IV. *Little Brown, Boston*, pp. 1-380, pls 1-19.

Allman G.J. 1874. Report on the Hydroida collected during the Expeditions of H.M.S. 'Porcupine'. *Transactions of the Zoological Society of London* 8: 469-481, pls 65-68.

Allman G. J. 1876. Diagnoses of new genera and species of Hydroida. *Journal of the Linnean Society of London* 12: 251-284, plates 9-23.

Allman G.J. 1877. Report on the Hydroida collected during the Exploration of the Gulf Stream by L. F. de Pourtalès, Assis-

tant United States Coast Survey. *Memoirs of the Museum of Comparative Zoology* 5: 1-66, plates 1-34.

Allman G. J. 1883. Report on the Hydroida dredged by H. M. S. Challenger during the years 1873-76. Part I Plumulariidae. *The Voyage of H. M. S. Challenger, Zoology* 20: 1-55, pl. 1-20.

Allman G.J. 1888. Report on the Hydroida dredged by H. M. S. Challenger during the years 1873-76. Part II.- The Tubularinae, Corymorphinae, Campanularinae, Sertularinae, and Thalamophora. *The Voyage of H. M. S. Challenger, Zoology* 70: 1-90.

Altuna A. 2012. New records of bathyal Leptolida (Cnidaria: Hydrozoa: Leptothecata) from the Bay of Biscay and the northwestern Iberian Peninsula (northeastern Atlantic). *Zootaxa* 3565: 1-17.

Altuna Prados A., Alvarez-Claudio C. 1994. The genus *Zygophylax* Quelch, 1885 (Cnidaria, Hydrozoa) in Biscay Bay. *Miscellanea Zoologica* 17: 1-16.

Ansín Agís J., Ramil F., Vervoort W. 2001. Atlantic Leptolida (Hydrozoa, Cnidaria) of the families Aglaopheniidae, Halopterididae, Kirchenpaueriidae and Plumulariidae collected during the CANCAP and Mauritania-II expeditions of the National Museum of Natural History, Leiden, the Netherlands. *Zoologische Verhandelingen, Leiden* 333: 1-268.

Ansín Agís J., Vervoort W., Ramil F. 2014. Hydroids of the families Kirchenpaueriidae Stechow, 1921 and Plumulariidae McCrady, 1859 (Cnidaria, Hydrozoa) collected in the Western Pacific Ocean by various French Expeditions. *Zoosystema* 36: 789-840.

Antsulevich A.E. 1988. Hydroids of the genus *Zygophylax* (Hydrozoa, Zygophylacidae) in the fauna of the USSR. *Zoologicheskii Zhurnal* 67: 123-127.

Bale W.M. 1884. Catalogue of the Australian hydroid zoophytes. *Sydney, Australian Museum Catalogue* No. 8: 1-198, plates 1-19.

Billard A. 1901. Note sur l'*Antennularia antennina* Lin. et sur l'*A. perrieri* n. sp. *Bulletin du Muséum national d'histoire naturelle* 7: 68-75.

Billard A. 1905. Note sur quelques hydroïdes de l'expédition du Travailleur. *Bulletin du Muséum national d'histoire naturelle* 11: 97-100.

Billard A. 1907. Hydroides de la Collection Lamarck du Muséum de Paris. I Plumulariidae. *Annales des sciences naturelles. Zoologie et biologie animale*, ser. 9, 5: 319-335.

Billard A. 1908a. Note sur deux variétés nouvelles d'Hydroides provenant de l'expédition du «Siboga». *Archives de Zoologie Expérimentale et Générale* (4) 8, Notes et Revue: LXXIII-LXXVII.

Billard A. 1908b. Sur les Plumulariidae de la collection du Challenger. *Comptes rendus hebdomadaires des séances de l'Académie des sciences de Paris* 147: 758-760, 938-941.

Billard A. 1909. Révision des espèces types d'hydroides de la collection Lamouroux. *Annales des Sciences naturelles, neuvième série, Zoologie* 9: 307-336.

Billard A. 1910. Révision d'une partie des Hydroïdes de la collection du British Museum. *Annales des Sciences naturelles, neuvième série, Zoologie* 11: 1-67.

Billard A. 1911. Note sur un nouveau genre et une nouvelle espèce d'Hydroïde: *Sibogella erecta*. *Archives de Zoologie Expérimentale et Générale, notes & revue* (5) 6: CVIII.

Billard A. 1913. Les Hydroïdes de l'expédition du SIBOGA. I Plumulariidae. *Siboga Expeditie* 7a: 1-115, pls 1-6.

- Billard A. 1918. Notes sur quelques espèces d'hydroïdes de l'expédition du Siboga. *Archives de Zoologie Expérimentale et Générale* 57, Notes et Revue: 21-27.
- Billard A. 1920. Note sur une espèce nouvelle d'Hydroïde: *Sertularella singularis*. *Archives de Zoologie Expérimentale et Générale, notes & revue* 59: 14-16.
- Billard A. 1925. Les hydroïdes de l'expédition du Siboga. II. Synthecidae et Sertularidae. *Siboga Expeditie* 7b: 117-232, 7 pls.
- Bouillon J., Gravili C., Pages F., Gili J.M., Boero F. 2006. An introduction to Hydrozoa. *Mémoires du Muséum National d'Histoire Naturelle* 194: 1-591.
- Bouillon J., Wouters K., Boero F. 1992. Etude des Solanderiidae de la Baie de Hansa (Papouasie Nouvelle-Guinée) avec une révision du genre *Solanderia* (Cnidaria, Hydrozoa). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie* 62: 5-33.
- Brinckmann-Voss A. 1970. Anthomedusae/Athecata (Hydrozoa, Cnidaria) of the Mediterranean. Part I. Capitata. *Fauna e Flora Golfo di Napoli* 39: 1-96, pls 1-11.
- Broch H. 1914. Hydrozoa benthonica. In: Michaelisen W. (Ed.), *Beiträge zur Kenntnis der Meeresfauna Westafrikas*, vol. 1, pp. 19-50, plate I. Friedrichsen, Hamburg.
- Busk G. 1852. An account of the Polyzoa, and the sertularian zoophytes, collected in the voyage of "Rattlesnake," on the coasts of Australia and the Louisiade Archipelago, ect. In: MacGillivray J., *Narrative of the voyage of H.M.S. Rattlesnake, commanded by late Captain Owen Stanley, R.N., F.R.S., etc., during the years 1846-1850*. Vol 1. Appendix 4. pp. 343-402. T. and W. Boone, London.
- Busk G. 1857. Zoophytology. *Quarterly Journal of Microscopical Science* 5: 172-174.
- Calder D.R. 1988. Shallow-water hydroids of Bermuda. The Athecatae. *Royal Ontario Museum Life Sciences Contributions* 148: 1-107.
- Calder D.R. 2010. Some anthoathecate hydroids and limnopolyps (Cnidaria, Hydrozoa) from the Hawaiian archipelago. *Zootaxa* 2590: 1-91.
- Calder D. 2013. Some shallow-water hydroids (Cnidaria: Hydrozoa) from the central east coast of Florida, USA. *Zootaxa* 3648: 1-72.
- Calder D.R., Mallinson J.J., Collins K., Hickman C.P. 2003. Additions to the hydroids (Cnidaria) of the Galapagos, with a list of species reported from the islands. *Journal of Natural History* 37: 1173-1218.
- Calder D.R., Vervoort W., Hochberg F.G. 2009. Lectotype designations of new species of hydroids (Cnidaria, Hydrozoa), described by C.M. Fraser, from Allan Hancock Pacific and Caribbean Sea Expeditions. *Zoologische Mededelingen* 83: 919-1054.
- Clarke S. F. 1894. The Hydroids. In: Report on the dredging operations off the west coast of Central America to the Galapagos, to the west coast of Mexico, and in the Gulf of California, in charge of Alexander Agassiz, carried out by the U.S. Fish Commission Steamer "Albatros", during 1891. Commander Z.L. Tanner, U.S.N., commanding. *Bulletin of the Museum of comparative Zoölogy of Harvard College* 25: 71-77, pls 1-5.
- Cornelius P.F.S. 1975. A revision of the species of Lafoeidae and Haleciidae (Coelenterata: Hydroida) recorded from Britain and nearby seas. *Bulletin of the British Museum* 28: 373-426.
- Cornelius P.F.S. 1992. Medusa loss in leptolid Hydrozoa (Cnidaria), hydroid rafting, and abbreviated life-cycles among their remote-island faunae: an interim review. *Scientia Marina* 56: 245-261.
- Cornelius P.F.S. 1995a. North-west European thecate hydroids and their medusae. Part 1. Introduction, Laodiceidae to Haleciidae. *Synopses of the British Fauna New Series* 50: 1-347.
- Cornelius P.F.S. 1995b. North-west European thecate hydroids and their medusae. Part 2. Sertulariidae to Campanulariidae. *Synopses of the British Fauna New Series* 50: 1-386.
- Di Camillo C.G., Bo M., Puce S., Bavestrello G. 2010. Association between *Dentitheca habereri* (Cnidaria: Hydrozoa) and two zoanthids. *Italian Journal of Zoology* 77: 81-91.
- Di Camillo C.G., Puce S., Bavestrello G. 2009. *Macrorhynchia* species (Cnidaria: Hydrozoa) from the Bunaken Marine Park (north Sulawesi, Indonesia) with a description of two new species. *Italian Journal of Zoology* 76: 208-228.
- Di Camillo C.G., Puce S., Bavestrello G. 2011. *Lytocarpia* and *Cladocarpus* (Cnidaria: Hydrozoa, Aglaopheniidae) from the Bunaken National Marine Park (North Sulawesi, Indonesia). *Marine Biodiversity* 41: 517-536.
- Esper E. J. C. 1788-1830. Die Pflanzenthieri in Abbildungen nach der Natur mit Farben erleuchtet nebst Beschreibungen. *Raspesche Buchhandlung, Nürnberg*. [Bound variably in several volumes] see <http://nbn-resolving.de/urn:nbn:de:bsz:16-diglit-28847>
- Fleming J. 1820. Observations on the natural history of the *Sertularia gelatinosa* of Pallas. *Edinburgh Philosophical Journal* 2: 82-89.
- Fraser C.M. 1918. *Monobrachium parasiticum* and other west coast hydroids. *Transaction of the Royal Society of Canada* (3)12: 131-138, pl. 1.
- Fraser C.M. 1935. Some Japanese hydroids, mostly new. *Proceedings and transactions of the Royal Society of Canada* (3) 29 sect. V: 105-112, pls 1-2.
- Fraser C.M. 1936. Some Japanese hydroids, mostly new. II. *Proceedings and transactions of the Royal Society of Canada* (3) 30 sect. 2: 49-54, pls. 1-2.
- Fraser C.M. 1937. Hydroids of the Pacific coast of Canada and the United States. *The University of Toronto Press, Toronto*. pp. 208, pls 1-44.
- Fraser C.M. 1938a. Hydroids of the 1934 Allan Hancock Pacific Expedition. *Allan Hancock Pacific Expeditions* 4: 1-105.
- Fraser C.M. 1938b. Hydroids of the 1932, 1933, 1935 and 1938 Allan Hancock Pacific Expeditions. *Allan Hancock Pacific Expeditions* 4: 129-153.
- Fraser C.M. 1940. Seven new species and one new genus of hydroids, mostly from the Atlantic Ocean. *Proceedings of the U.S. national Museum* 88: 575-580, pls 32-33.
- Galea H.R. 2008. On a collection of shallow-water hydroids (Cnidaria: Hydrozoa) from Guadeloupe and Les Saintes, French Lesser Antilles. *Zootaxa* 17: 1-54.
- Galea H.R. 2010. Notes on a small collection of thecate hydroids (Cnidaria: Hydrozoa) from Tristan da Cunha, south Atlantic. *Zootaxa* 2336: 1-18.
- Galea H.R. 2013. New additions to the shallow-water hydroids (Cnidaria: Hydrozoa) of the French Lesser Antilles: Martinique. *Zootaxa* 3686: 1-50.
- Gibbons M.J., Ryland J.S. 1989. Intertidal and shallow water hydroids from Fiji. 1. Athecata to Sertulariidae. *Memoirs of the Queensland Museum* 27: 377-432.
- Goldfuss G.A. 1820. Handbuch der Zoologie. Erste Abteilung. *Schrag, Nürnberg*, pp. 1-696.
- Grasshoff M., Scheer G. 1991. Die Publikationsdaten von E.J.C. Esper „Die Pflanzenthieri“. *Senckenbergiana Biologica* 71: 191-208.

- Gray J.E. 1848. List of the specimens of British animals in the collection of the British Museum. Part 1. Centroniae or radiated animals. *British Museum, London*, pp. 173.
- Hargitt C.W. 1924. Hydroids of the Philippine Islands. *Philippine Journal of Science* 24: 467-507, pls 1-6.
- Hickson S.J. 1903. On the Coelenterata collected by Mr. C. Crossland in Zanzibar. - I. *Ceratella minima*, n. sp. *Proceedings of the Zoological Society of London* 1903: 113-116, pl. 13.
- Hincks T. 1868. A history of the British hydroid zoophytes. *John van Voorst, London*. Volume 1: pp. i-lxvii + 1-338. Volume 2: pls 1-67.
- Hincks T. 1874. Notes on Norwegian Hydroida from deep water. *Annals and Magazine of Natural History* (4) 13: 125-137.
- Hirohito Emperor of Japan 1967. A review of the hydroids of the family Clathrozonidae with description of a new genus and species from Japan. *Biological Laboratory of the Imperial Household, Tokyo*, pp. i-iv, 1-14, frontispiece, pls 1-14, map.
- Hirohito Emperor of Japan 1969. Some hydroids from the Amakusa Islands. *Biological Laboratory of the Imperial Household, Tokyo*, pp. 1-32.
- Hirohito Emperor of Japan 1971. Additional notes on *Clathrozon wilsoni* Spencer. *Biological Laboratory of the Imperial Household, Tokyo*, pp. 1-5, frontispiece, pls. 1-4, tab. 1. [separately paginated Japanese summary]
- Hirohito Emperor of Japan 1977. Five Hydroid Species from the Gulf of Aqaba, Red Sea. *Biological Laboratory of the Imperial Household, Tokyo*, pp. 1-26, pls 1-3.
- Hirohito Emperor of Japan 1983. Hydroids from Izu Oshima and Nijima. *Biological Laboratory of the Imperial Household, Tokyo*, pp. 1-83.
- Hirohito Emperor of Japan 1988. The hydroids of Sagami Bay collected by His Majesty the Emperor of Japan. *Biological Laboratory Imperial Household, Tokyo*, pp. 1-179, plates 1-4.
- Hirohito Emperor of Japan 1995. The hydroids of Sagami Bay II. Thecata. *Biological Laboratory of the Imperial Household, Tokyo*, pp. 354, 13 pls.
- Hirose M., Hirose E. 2012. A new species of *Zanclaea* (Cnidaria: Hydrozoa) associated with scleractinian corals from Okinawa, Japan. *Journal of the Marine Biological Association of the United Kingdom* 92: 877-884.
- Inaba M. 1890. Hydroida collected at Misaki, Miura, Soshu [in Japanese]. *Zoological Magazine, Tokyo* 2: 425-431. See <http://www.biodiversitylibrary.org/item/42122#page/422/mode/lup>.
- Inaba M. 1892. The hydroids collected at Misaki, Miura, Soshu [in Japanese]. *Zoological Magazine, Tokyo* 4: 93-101, 124-131. See <http://www.biodiversitylibrary.org/item/42242#page/114/mode/lup>.
- Jäderholm E. 1896. Über aussereuropäische Hydroiden des zoologischen Museums der Universität Upsala. *Bihang till Kongliga Svenska Vetenskaps-akademiens handlingar Afd. 4* 6: 1-20, pls 1-2.
- Jäderholm E. 1903. Aussereuropäische Hydroiden im schwedischen Reichsmuseum. *Arkiv för Zoologi* 1: 259-312, pls 12-15.
- Jäderholm E. 1919. Zur Kenntnis der Hydroidenfauna Japans. *Arkiv för Zoologi* 12: 1-34, pls 1-6.
- Jäderholm E. 1920. On some exotic hydroids in the Swedish Zoological State Museum. *Arkiv för Zoologi* 13: 1-11, pls 1-2.
- Jäderholm E. 1923. Notes on hydroids from the Great Ocean. *Göteborgs Kungliga Vetenskaps- och Vitterhets-Samhället Handlingar* 26: 1-6.
- Jäderholm E. 1926. Über einige antarktische und subantarktische Hydroiden. *Arkiv för Zoologi* 18: 1-7.
- Kirchenpauer G.H. 1876. Ueber die Hydroidenfamilie Plumulariidae, einzelne Gruppen derselben und ihre Fruchtbehälter. II. *Plumularia* und *Nemertesia*. *Abhandlungen aus dem Gebiet der Naturwissenschaften, herausgegeben von dem naturwissenschaftlichen Verein in Hamburg* 6: 1-59, pls 1-8.
- Kirkendale L., Calder D.R. 2003. Hydroids (Cnidaria: Hydrozoa) from Guam and the Commonwealth of the Northern Marianas Islands (CNMI). *Micronesica* 36: 159-188.
- Kirkpatrick R. 1890. Report upon the Hydrozoa and Polyzoa collected by P.W. Bassett-Smith, Esq., Surgeon R.N., during the survey of the Tizard and Macclesfield Banks, in the China Sea, by H.M.S. "Rambler", commander W.U. Moore. *Annals and Magazine of Natural History* (6) 5: 11-24.
- Kubota S. 1987. Occurrence of a bivalve-inhabiting hydroid *Eugymnanthea inquilina japonica* Kubota from Okinawa Island, southwest of Japan, with notes on parthenogenesis. *Galaxea* 6: 31-34.
- Lamarck J.B. 1816. Histoire naturelle des animaux sans vertèbres. *Verdière, Paris*. pp. 568.
- Lamoureux J.V.F. 1812. Extrait d'un mémoire sur la classification des polypes coralligènes non entièrement pierreux. *Nouveau Bulletin des Sciences par la Société Philomatique de Paris* 3: 181-188.
- Lamoureux J.V.F. 1816. Histoire des polypiers coralligènes flexibles, vulgairement nommés zoophytes. *F. Poisson, Caen*, pp. i-xxxiv, 1-560.
- Lamoureux J.V.F. 1821. Exposition méthodique des genres de l'ordre des polypiers, avec leur description et celle des principales espèces, figurées dans 84 planches, les 63 premières appartenant à l'histoire naturelle des zoophytes d'Ellis et Solander. *Agasse, Paris*, pp. i-viii, 1-115, pls. 1-84.
- Leloup E. 1930. Coelentérés hydropolypes. In: Résultats Scientifiques du Voyage aux Indes Orientales Néerlandaises de LL. AA. RR. le Prince et la Princesse Léopold de Belgique. *Mémoires du Musée royal d'histoire naturelle de Belgique*, hors série 2: 1-18, pl. 1.
- Leloup E. 1938. Quelques hydropolypes de la baie de Sagami, Japon. *Bulletin du Musée royal d'histoire naturelle de Belgique* 14: 1-22.
- Linnaeus C. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Editio decima, reformata. *Laurentii Salvii, Holmiae*, pp. ii + 824.
- Marktanner-Turneretscher G. 1890. Hydroiden des K. & K. Naturhistorischen Hofmuseums. *Annalen des K. K. Naturhistorischen Hofmuseums* 5: 195-286.
- McCrary J. 1859. Gymnophthalmata of Charleston Harbor. *Proceedings of the Elliott Society of Natural History* 1: 103-221, pls 8-12.
- Millard N.A.H. 1962. The Hydrozoa of the south and west coasts of South Africa. Part I. The Plumulariidae. *Annals of the South African Museum* 46: 261-319.
- Millard N.A.H. 1975. Monograph on the Hydroida of southern Africa. *Annals of the South African Museum* 68: 1-513.
- Millard N.A.H. 1977. The South African Museum's Meiring Naude cruises. Part 3. Hydroida. *Annals of the South African Museum* 73(5): 105-131.

- Millard N.A.H., Bouillon J. 1973. Hydroids from the Seychelles (Coelenterata). *Annales du Musée Royal de l'Afrique Centrale, série In-8°, Sciences Zoologiques* 206: 1-106, pls 1-5.
- Moura C.J., Cunha M.R., Porteiro F.M., Rogers A.D. 2011. Polyphyly and cryptic diversity in the hydrozoan families Lafoeidae and Hebellidae (Cnidaria: Hydrozoa). *Invertebrate Systematics* 25: 454-470.
- Moura C.J., Cunha M.R., Porteiro F.M., Yesson C., Rogers A.D. 2012. Evolution of *Nemertesia* hydroids (Cnidaria: Hydrozoa, Plumulariidae) from the shallow and deep waters of the NE Atlantic and western Mediterranean. *Zoologica Scripta* 41: 79-96.
- Naumov D.V. 1969. Hydroids and Hydromedusae of the USSR. Israel Program for scientific translation, Jerusalem, pp. 463, 30 plates.
- Norman A.M. 1875. In: J.G. Jeffreys & A.M. Norman, Submarine-cable fauna. *Annals and Magazine of Natural History* (4) 15: 169-176, pl. 12.
- Nutting C.C. 1906. Hydroids of the Hawaiian Islands collected by the steamer Albatross in 1902. *Bulletin of the United States Fish Commission for 1903* 23: 931-959, pls 1-13.
- Nutting C.C. 1927. Report on Hydroida collected by the United States Fisheries steamer Albatross in the Philippine region 1910. In: Contributions to the biology of the Philippine Archipelago and adjacent regions, part 3. *Bulletin of the United States National Museum* 100: 195-242.
- Oestman C., Piraino S., Kem W. 1991. Nematocysts of the Mediterranean hydroid *Halocordyle disticha*. *Hydrobiologia* 217: 607-613.
- Park J.H. 2010. Cnidaria: Hydrozoa: Thecatae. Thecates. *Invertebrate fauna of Korea* 4(1): 1-183.
- Peña Cantero A.L., Marques A.C., Migotto A.E. 2004. Redescription of *Acryptolaria normani* Nutting, 1927, junior synonym of the Western Pacific species *Zygophylax tizardensis* Kirkpatrick, 1890 (Cnidaria: Hydrozoa: Lafoeidae). *Raffles Bulletin of Zoology* 52: 1-6.
- Peña Cantero A.L., Marques A.C., Migotto A.E. 2007. Revision of the genus *Acryptolaria* Norman, 1875 (Cnidaria, Hydrozoa, Lafoeidae). *Journal of Natural History* 41: 229-291.
- Peña Cantero A.L., Ramil F. 2006. Benthic hydroids associated with volcanic structures from Bransfield Strait (Antarctica) collected by the Spanish Antarctic expedition GEBRAP96. *Deep Sea Research Part II* 53(8-10): 949-958.
- Peña Cantero A.L., Sentandreu V., Latorre A. 2010. Phylogenetic relationships of the endemic Antarctic benthic hydroids (Cnidaria, Hydrozoa): what does the mitochondrial 16S rRNA tell us about it? *Polar Biology* 33: 41-57.
- Peña Cantero A.L., Vervoort W. 1999. Review of the genus *Schizotricha* Allman, 1883 (Cnidaria, Hydrozoa, Halopterididae). *Journal of Natural History* 33: 351-386.
- Peña Cantero A.L., Vervoort W. 2010. Species of *Acryptolaria* Norman, 1875 (Cnidaria, Hydrozoa, Lafoeidae) collected in the Western Pacific by various French expeditions, with the description of nineteen new species. *Zoosystema* 32: 267-332.
- Peña Cantero A.L., Vervoort W., Watson J. E. 2003. On Clathrozoellidae (Cnidaria, Hydrozoa, Anthoathecatae), a new family of rare deep-water leptolids, with the description of three new species. *Zoologische Verhandelingen* 345: 281-296.
- Pictet C., Bedot M. 1900. Hydraires provenant des campagnes de l'Hirondelle (1886-1888). *Résultats des campagnes scientifiques accomplies sur son yacht par Prince Albert 1^{er} de Monaco* 18: 1-59.
- Queich J.J. 1885. On some deep-sea and shallow-water Hydrozoa. *Annals and Magazine of Natural History* (5) 16: 1-20, pls 1-2.
- Ralph P.M. 1958. New Zealand thecate hydroids. Part II.- Families Lafoeidae, Lineolariidae, Haleciidae and Synthechiidae. *Transactions of the Royal Society of New Zealand* 85: 301-356.
- Ralph P.M. 1961. New Zealand thecate hydroids. Part III.- Family Sertulariidae. *Transactions of the Royal Society of New Zealand* 88: 749-838.
- Ramil F., Vervoort W. 1992a. Report on the Hydroida collected by the 'BALGIM' expedition in and around the Strait of Gibraltar. *Zoologische Verhandelingen* 277: 1-262.
- Ramil F., Vervoort W. 1992b. Some consideration concerning the genus *Cladocarpus* (Cnidaria: Hydrozoa). *Scientia Marina* 56: 171-176.
- Rees W.J., Vervoort W. 1987. Hydroids from the John Murray Expedition to the Indian Ocean, with revisory notes on *Hydrodendron*, *Abietinella*, *Cryptolaria* and *Zygophylax* (Cnidaria: Hydrozoa). *Zoologische Verhandelingen, Leiden* 237: 1-209.
- Rho B.J. 1967. Marine hydroids from the West and South Sea of Korea. *Korean Culture Research Institute* 10: 341-360.
- Ritchie J. 1909. Supplementary reports on the hydroids of the Scottish National Antarctic Expedition. *Transactions of the Royal Society of Edinburgh* 47: 65-101.
- Ritchie J. 1911. Hydrozoa (hydroid zoophytes and Stylasterina) of the "Thetis" expedition. *Memoir / Australian Museum* 4: 807-869.
- Ruthensteiner B., Reinicke G.B., Straube N. 2008. The type material of Hydrozoa described by Eberhard Stechow in the Zoologische Staatssammlung München. *Spixiana* 31(1): 3-27.
- Ryland J.S., Gibbons M.J. 1991. Intertidal and shallow water hydroids from Fiji. 2. Plumulariidae and Aglaopheniidae. *Memoirs of the Queensland Museum* 30: 525-560.
- Schuchert P. 1996. The marine fauna of New Zealand: athecate hydroids and their medusae (Cnidaria: Hydrozoa). *New Zealand Oceanographic Institute Memoir* 106: 1-159.
- Schuchert P. 1997. Review of the family Halopterididae (Hydrozoa, Cnidaria). *Zoologische Verhandelingen, Leiden* 309: 1-162.
- Schuchert P. 2001. Hydroids of Greenland and Iceland (Cnidaria, Hydrozoa). *Meddelelser om Grønland, Bioscience* 53: 1-184.
- Schuchert P. 2003. Hydroids (Cnidaria, Hydrozoa) of the Danish expedition to the Kei Islands. *Steenstrupia* 27: 137-256.
- Schuchert P. 2006. The European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Capitata Part 1. *Revue suisse de Zoologie* 113: 325-410.
- Schuchert P. 2012. North-West European Athecate Hydroids and their Medusae. Synopses of the British Fauna (New Series) 59. *The Linnean Society of London, London*, pp. i-viii, 1-364.
- Schuchert P. 2014. High genetic diversity in the hydroid *Plumularia setacea*: A multitude of cryptic species or extensive population subdivision? *Molecular Phylogenetics and Evolution* 76: 1-9.
<http://dx.doi.org/10.1016/j.ympev.2014.02.020>
- Schuchert P. 2015. World Hydrozoa database. Accessed at <http://www.marinespecies.org/hydrozoa> on 26 January 2015.
- Spalding M.D., Fox H.E., Allen G.R., et al. 2007. Marine

- Ecoregions of the World: a bioregionalization of coast and shelf areas. *BioScience* 57: 573-583.
- Spencer W.B. 1891. A new family of Hydroidea, together with a description of the structure of a new species of *Plumularia*. *Transactions of the Royal Society of Victoria* 2: 121-140, pls 17-23.
- Spletstösser W. 1929. Beiträge zur Kenntnis der Sertulariiden. *Thyroscyphus* Allm., *Cnidoscyphus* nov. gen., *Parascyphus* Ritchie. *Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere* 58: 1-134.
- Stechow E. 1908. Neue japanische Athecata und Plumulariidae aus der Sammlung Dr. Doflein. *Zoologischer Anzeiger* 32: 192-200.
- Stechow E. 1909. Hydroidpolypen der japanischen Ostküste. I. Teil: Athecata und Plumularidae. In: F. Doflein, Beiträge zur Naturgeschichte Ostasiens. *Abhandlungen der Mathematisch-Physikalischen Klasse der Königlich Bayerischen Akademie der Wissenschaften, Supplement Band 1*: 1-111, plates 1-7.
- Stechow E. 1913. Hydroidpolypen der japanischen Ostküste. II. Teil: Campanularidae, Halecidae, Lafoeidae, Campanuliniidae und Sertularidae, nebst Ergänzungen zu den Athecata und Plumularidae. In: Doflein F., Beiträge zur Naturgeschichte Ostasiens. *Abhandlungen der Mathematisch-Physikalischen Klasse der Königlich Bayerischen Akademie der Wissenschaften, Supplement Band 3*: 1-162.
- Stechow E. 1919. Zur Kenntnis der Hydroidenfauna des Mittelmeeres, Amerikas und anderer Gebiete, nebst Angaben über einige Kirchenpauer'sche Typen von Plumulariden. *Zoologische Jahrbücher. Abteilung für Systematik, Geographie und Biologie der Tiere* 42: 1-172.
- Stechow E. 1920. Neue Ergebnisse auf dem Gebiete der Hydroidenforschung. *Sitzungsberichte der Gesellschaft für Morphologie und Physiologie in München* 31: 9-45.
- Stechow E. 1921. Neue Genera und Species von Hydrozoen und anderen Evertibraten. *Archiv für Naturgeschichte* 87: 248-265.
- Stechow E. 1922. Zur Systematik der Hydrozoen, Stromatoporen, Siphonophoren, Anthozoen und Ctenophoren. *Archiv für Naturgeschichte* 88: 141-155.
- Stechow E. 1923a. Neue Hydroiden der Deutschen Tiefsee-Expedition, nebst Bemerkungen über einige andere Formen. *Zoologischer Anzeiger* 56: 1-20.
- Stechow E. 1923b. Die Hydroidenfauna der japanischen Region. *Journal of the College of Science of the imperial University of Tokyo* 44: 1-23.
- Stechow E. 1923c. Zur Kenntnis der Hydroidenfauna des Mittelmeeres, Amerikas und anderer Gebiete. II. Teil. *Zoologische Jahrbücher, Abteilung für Systematik, Geographie und Biologie der Tiere* 47: 29-270.
- Stechow E. 1925. Hydroiden der Deutschen Tiefsee-Expedition. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee Expedition „Valdivia“* 17: 383-546.
- Thornely L.R. 1908. Reports on the Marine Biology of the Sudanese Red Sea. X. Hydroida collected by Mr. C. Crossland from October 1904 to May 1905. *The Journal of the Linnean Society of London. Zoology* 31: 80-85, pl. 9.
- Totton A.K. 1930. Coelenterata. Part V.- Hydroida. *British Antarctic („Terra Nova“) Expedition, 1910, Natural History Report, Zoology* 5: 131-252, pls 1-3.
- Versluys J.J. 1899. Hydraires calyptoblastes recueillis dans la mer des Antilles, pendant l'une des croisières accomplies par le comte R. de Dalmas sur son yacht «CHAZALIE». *Mémoires de la Société Zoologique de France* 12: 29-58.
- Vervoort W. 1941. The Hydroida of the Snellius Expedition (Milleporidae and Stylasteridae excluded). Biological results of the Snellius Expedition XI. *Temminckia* 6: 186-240.
- Vervoort W. 1966. Bathyal and abyssal hydroids. *Galathea Report* 8: 97-173.
- Vervoort W. 1967. The Hydroida and Chondrophora of the Israel South Red Sea Expedition. In: Israel South Red Sea Expedition Reports, No. 25. *Bulletin of the Sea Fisheries Research Station of Israel* 43: 18-54.
- Vervoort W. 1972. Hydroids from the Theta, Vema and Yelcho cruises of the Lamont-Doherty geological observatory. *Zoologische Verhandelingen, Leiden* 120: 1-247.
- Vervoort W. 1993. Cnidaria, Hydrozoa, Hydroida: hydroids from the Western Pacific (Philippines, Indonesia and New Caledonia). 1: Sertulariidae (Part 1). *Mémoires du Muséum National d'Histoire Naturelle* 158: 89-298.
- Vervoort W. 2006. Leptolida (Cnidaria: Hydrozoa) collected during the CANCAP and Mauritania-II expeditions of the National Museum of Natural History, Leiden, the Netherlands (Anthoathecata, various families of Leptothecata and addenda). CANCAP-project. Contributions, no. 128. *Zoologische Mededelingen, Leiden* 80: 181-318.
- Vervoort W., Vasseur P. 1977. Hydroids from French Polynesia with notes on distribution and ecology. *Zoologische Verhandelingen, Leiden* 159: 3-98.
- Vervoort W., Watson J.E. 2003. The marine fauna of New Zealand: Leptothecata (Cnidaria: Hydrozoa) (thecate hydroids). *NIWA Biodiversity Memoir* 119: 1-538.
- von Campenhausen B. 1896a. 2. Hydroiden von Ternate, nach den Sammlungen Prof. W. Kükenthal's. *Zoologischer Anzeiger* 19: 103-107.
- von Campenhausen B. 1896b. Hydroiden von Ternate. In: Kükenthal W., Ergebnisse einer zoologischen Forschungsreise in den Molluken und Borneo, Theil 2. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 23: 297-320, pl. 15.
- Watson J.E. 1999. Hydroids (Hydrozoa: Anthoathecata) from the Beagle Gulf and Darwin Harbour, northern Australia. *The Beagle, Records of the Museums and Art Galleries of the Northern Territory* 15: 1-21.
- Watson J.E. 2000. Hydroids (Hydrozoa: Leptothecatae) from the Beagle Gulf and Darwin Harbour, northern Australia. *The Beagle, Records of the Museums and Art Galleries of the Northern Territory* 16: 1-82.
- Watson J.E. 2005. Hydroids of the Archipelago of the Recherche and Esperance, Western Australia: Annotated list, redescription of species and description of new species. In: Wells F. E., Walker D. I., Kendrick, G. A. (Eds), The Marine Flora and Fauna of Esperance, Western Australia, pp. 495-612. *Western Australian Museum, Perth*.
- Watson J.E., Vervoort W. 2001. The hydroid fauna of Tasmanian seamounts. *Zoologische Verhandelingen* 334: 151-187.
- Whitelegge T. 1899. The Hydrozoa, Scyphozoa, Actinozoa, and Vermes of Funafuti. In: The atoll of Funafuti, Elliot Group; its zoology, botany, ethnology, and general structure based on collections made by Mr. Charles Hedley of the Australian Museum, Sydney, N.S.W. *Memoirs of the Australian Museum* 3: 371-394, pls 23-27.
- Yamada M., Kubota S. 1987. Preliminary report on the marine hydroid fauna in Okinawa Islands. *Galaxea* 6: 35-42.